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THE UNIVERSITY OF ALBERTA

Morphology, systematics and ecology of mountain midges (Diptera: Deuterophlebiidae).

by

© Gregory W. Courtney

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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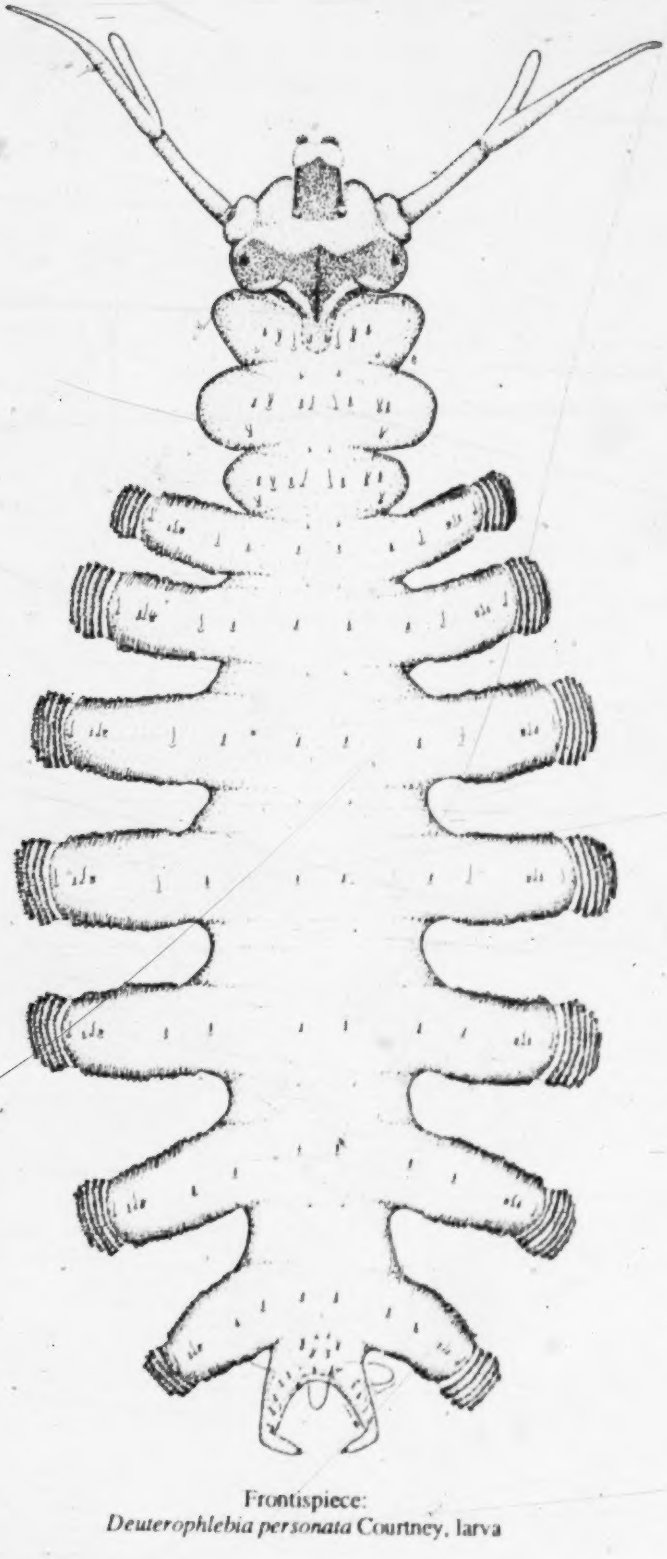

Frontispiece:
Deuterophlebia personata Courtney, larva

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the faculty of Graduate Studies and Research for acceptance, a thesis entitled: Morphology, systematics and ecology of mountain midges (Diptera: Deuterophlebiidae), submitted by Gregory W. Courtney in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

D. A. Craig
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Date 10 Aug 1989

ABSTRACT

Mountain midges (Diptera: Deuterophlebiidae) are an enigmatic group of aquatic insects from the western Nearctic and eastern Palaearctic. Deuterophlebiids are rheophilic specialists, characterized by numerous features that permit life in or near torrential streams. A morphological study of larval Deuterophlebiidae emphasizes cranial and mouthpart structure. Included is a discussion of feeding behaviour and how differing mouthpart structure influences food acquisition.

Phylogenetic analysis of larval, pupal and adult features of the Deuterophlebiidae and other Diptera provides support for: (1) monophyly of the Blephariceroidea (= Deuterophlebiidae + Blephariceridae); (2) monophyly of the Blephariceromorpha (= Nymphomyiidae + (Deuterophlebiidae + Blephariceridae); and (3) a sister-group relationship between the Blephariceromorpha and Psychodomorpha.

Taxonomic revision of the Deuterophlebiidae includes descriptions of six new species. Four are Palaearctic: *D. bicarinata* sp. nov., *D. brachyrhina* sp. nov., *D. oporina* sp. nov., and *D. blepharis* sp. nov.; and two Nearctic: *D. personata* sp. nov. and *D. vernalis* sp. nov.. A lectotype is designated for *D. mirabilis* Edwards, and a lectotype and paralectotype are designated for *D. coloradensis* Pennak. Also provided are distributional data and keys to larvae, pupae, and adults for all species, and a general discussion of character variation.

Ecological investigations emphasize habitat requirements, reproductive biology, and phenologies. Adult deuterophlebiids show marked diel synchrony, with emergence, flight, and mating during the early morning. Females shed their wings and actively search for beneath-water oviposition sites. Most Nearctic deuterophlebiids have univoltine, asynchronous life histories. This is adaptive for populations in a region where frequent, unpredictable rains may cause flooding, substrate scouring, and high mortality. Temporal isolation of torrenticolous insect populations was evident, especially among sympatric deuterophlebiids and blephariceids.

Cladistic analysis of larval, pupal, and adult characters provides a framework for discussion about the phylogenetic relationships and geographical history of species of Deuterophlebiidae. Based on features of adult males, *D. brachyrhina* is proposed as the sister taxon of all other deuterophlebiids, with *D. oporina* the sister taxon of the latter. Relationships between derivative species are based mostly on larval and pupal characters, and provide a basis for alternate phylogenetic reconstructions. Preliminary zoogeographic analyses suggests that Nearctic deuterophlebiids originated from at least two invasions of North America.

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1. INTRODUCTION

Mountain midges (Diptera: Deuterophlebiidae) are an enigmatic family of nematocerous flies from western North America and eastern and central Asia. Their immature stages are rheophilic specialists, possessing a variety of morphological features that permit life in swiftly flowing, often torrential, streams. Among these adaptations are eversible, crochet-tipped larval prolegs and a dorsoventrally compressed, streamlined pupa. Adults, which lack functional mouthparts and survive for only a few hours, exhibit equally aberrant features. Deuterophlebiids are of interest to both aquatic entomologist and dipterist, not only for their morphological and ecological specializations, but because the family is considered a primitive lineage of Diptera (Hennig 1973; McAlpine *et al.* 1981). Unfortunately, there is a significant lack of biological information about these unusual flies.

Morphological studies of the Deuterophlebiidae are few, with most limited to general descriptions of external characteristics, and little (Edwards 1922; Pulikovsky 1924; Hora 1930) or no (Brodsky 1930; Kitakami 1938; Pennak 1945; Kennedy 1958, 1960) comparative or phylogenetic interpretation. Previous investigations of the structure and higher classification of Diptera provide few insights about the phylogenetic position of the Deuterophlebiidae. Rohdendorf (1964, 1974) failed to root the Deuterophlebiidae to the rest of the Diptera, though he considered the family isolated enough to place it in a separate and primitive infraorder, the Deuterophlebiomorpha. Based on rather tenuous grounds, Hennig (1973) treated the Deuterophlebiidae and Blephariceridae as a monophyletic clade, within the infraorder Psychodomorpha. Cutten and Kevan (1970) suggested affinities between the Deuterophlebiidae and Nymphomyiidae, and McAlpine *et al.* (1981) implied that the Blephariceridae, Deuterophlebiidae, and Nymphomyiidae form a monophyletic group (infraorder Blephariceromorpha). Wood and Borkent (*in press*) recently formalized the latter hypothesis, proposing further that the Nymphomyiidae and Blephariceroidea (= Deuterophlebiidae + Blephariceridae) are sister taxa. Past attempts to place all of these families in a phylogenetic system have been confounded by the prevalence of unique, derived (*i.e.*, autapotypic) characters, and has generally led to the conclusion that these taxa are phylogenetically "isolated" and "primitive". Furthermore, life in similar physical conditions (*i.e.*, swiftly flowing streams) may be responsible for substantive structural convergence (Hora 1930). Definitive conclusions about the phylogenetic relationships among these families and other Diptera requires detailed morphological studies of all life stages, with emphasis on features that can be compared across family lines.

The taxonomic history of the Deuterophlebiidae has been mostly one of isolated species descriptions and range extensions, with few attempts to synthesize information in a comprehensive morphological, taxonomic, or phylogenetic context. Prior to this investigation, the Deuterophlebiidae contained eight described species, four each from eastern Asia (Edwards 1922; Kitakami 1938; Jedlicka & Halgos 1981) and western North America (Pennak 1945; Wirth 1951; Kennedy 1958, 1960). The present investigation of the systematics and ecology of mountain midges has led to the discovery of several new species, including two from western North America, and four from eastern and central Asia. These new findings are presented in the context of a re-evaluation of the classification of species of *Deuterophlebia*.

Interest in the adaptations and ecology of rheophilic, or current-loving, organisms has grown rapidly in recent years. Deuterophlebiids are among these rheophilic specialists, as all life stages are intimately associated with torrenticolous habitats. Except for work by Yie (1933) and Kennedy (1958), most published information about mountain midge ecology has been in the form of brief mention of habitat or life histories, mostly in the context of species descriptions or geographic range extensions. Very little is known about the reproductive biology of mountain midges, particularly with regard to mating behaviour and oviposition. Information about deuterophlebiid phenologies is also lacking, partly because of the difficulty in sampling for early instar larvae.

This thesis summarizes investigations of the structure, classification, and ecology of mountain midges. Five separate papers are presented as the following chapters: (2) Cuticular morphology of larval mountain midges (Diptera: Deuterophlebiidae): implications for the phylogenetic relationships of Nematocera; (3) Phylogenetic analysis of the Blephariceromorpha, with special reference to mountain midges (Diptera: Deuterophlebiidae); (4) Taxonomic revision of mountain midges (Diptera: Deuterophlebiidae); (5) Ecological studies of Nearctic mountain midges (Diptera: Deuterophlebiidae), with emphasis on habitat characteristics, reproductive biology and phenologies; and (6) Phylogenetic and zoogeographic relationships of the world species of mountain midges (Diptera: Deuterophlebiidae).

Chapter 2 provides a detailed description of, and standard terms for, cuticular structures of larval Deuterophlebiidae. Emphasis is on features of the head and mouthparts, including homologies of cranial musculature. Morphological features of larval Deuterophlebiidae and other Nematocera, particularly the Blephariceridae, are compared by cladistic methods (*sensu* Hennig 1966), providing a test of various phylogenetic hypotheses (especially Wood and Borkent *in press*).

Chapter 3 takes the above analysis one step further, presenting a cladistic analysis of characters from all life stages (*i.e.*, larvae, pupae, and adults), and testing the phylogenetic hypotheses of Rohdendorf (1964, 1974), Hennig (1973), and Wood and Borkent (*in press*). In particular, monophyly of the Blephariceromorpha (*sensu* Wood and Borkent *loc. cit.*) and its constituent families, and their relationship to other Diptera, is evaluated. A second goal is to test the hypothesized sister group relationship of Deuterophlebiidae and Blephariceridae, thus establishing a framework for subsequent phylogenetic analyses of the Deuterophlebiidae (Chapter 6).

Chapter 4 presents a taxonomic revision of of mountain midges, including diagnoses, descriptions, distributional data, and bionomical and taxonomic notes about new and existing species, and a general discussion of structural variation in the family.

Several new character systems are introduced, and serve as a basis for keys to the identification of larvae, pupae and adults of world species of *Deuterophlebia*.

Chapter 5 provides information about collecting techniques, and a review of deuterophlebiid ecology, with emphasis on habitat characteristics, reproductive biology and phenologies. Included is a discussion of larval instar determination and adult emergence times, behaviour, sex ratios, and longevity. Mating and oviposition hypotheses are also evaluated. Phenological studies of deuterophlebiid populations from the Pacific Northwest are summarized, and serve as a basis for a general discussion about life history adaptations of torrenticolous organisms.

The last paper in this thesis (Chapter 6) summarizes a phylogenetic investigation of constituent species of the Deuterophlebiidae. A cladistic analysis of larval, pupal, and adult characters provides a framework for discussion about the evolution and zoogeography of the world species of mountain midges.

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2. CUTICULAR MORPHOLOGY OF LARVAL MOUNTAIN MIDGES (DIPTERA: DEUTEROPHLEBIIDAE): IMPLICATIONS FOR THE PHYLOGENETIC RELATIONSHIPS OF NEMATOCERA.[1]

2.1 Synopsis

The cuticular structure of larval mountain midges (Diptera: Deuterophlebiidae) is described, with emphasis on the cranium and mouthparts. Homologies are suggested for musculature and external features of the head capsule. External features of the thorax and abdomen are described, and a system for deuterophlebiid larval chaetotaxy presented. Also included is a discussion of feeding behaviour of Deuterophlebiidae and Blephariceridae larvae, and how differing morphological characteristics influence mechanisms of food acquisition. Structural features for larvae of the Deuterophlebiidae and other Nematocera provides support for: (1) a sister-group relationship between the Deuterophlebiidae and Blephariceridae; (2) a monophyletic Blephariceromorpha composed of the Nymphomyiidae + (Deuterophlebiidae + Blephariceridae); and (3) a sister-group relationship between the Blephariceromorpha and Psychodomorpha.

2.2 Introduction

Since first discovered more than 60 years ago (Edwards 1922), mountain midges (Diptera: Deuterophlebiidae) have remained a phylogenetic and ecological enigma. The family contains eight described species, four each from eastern Asia (Edwards 1922; Kitakami 1938; Jedlicka and Halgos 1981) and western North America (Pennak 1945; Wirth 1951; Kennedy 1958, 1960), and several undescribed species from both regions (see chapter 4). Larvae and pupae occur on rocky substrates in running water, often where mainstream current velocities exceed 2m/s (*personal observation*; Brodsky 1980).

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[1] A version of this chapter has been accepted for publication in the *Canadian Journal of Zoology*.

Relatively few insects have invaded these habitats and, in most instances, morphological and ecological specialization is apparent (Hora 1930).

Noteworthy among torrenticolous specialists are the dipteran families Blephariceridae and Deuterophlebiidae. Both are considered primitive lineages of Diptera (Hennig 1973; Rohdendorf 1974; McAlpine *et al.* 1981), though few studies have discussed characters supporting this hypothesis. The two families share a number of structural features (*e.g.*, lateral prolegs on larval abdomen, pupal shape and attachment devices, secondary wing folds in adult), and common ancestry has been proposed (Hennig 1973). An alternate hypothesis is morphological convergence due to life in similar physical conditions (Pulikovsky 1924; Hora 1930; Hogue 1987). Hennig (1973) tentatively placed the Deuterophlebiidae and Blephariceridae in the infraorder Psychodomorpha, an assemblage of families also including Psychodidae, Nymphomyiidae, Tanyderidae and Ptychopteridae. Cutten and Kevan (1970) suggested Deuterophlebiidae and Nymphomyiidae are closely related, and McAlpine, *et al.* (1981) presented a classification which implied that the Blephariceridae + Deuterophlebiidae + Nymphomyiidae form a monophyletic group (infraorder Blephariceromorpha). Wood and Borkent (*in press*) formalized the latter hypothesis, proposing further that the Nymphomyiidae are the sister group of the Blephariceroidea (= Deuterophlebiidae + Blephariceridae). Evaluating these hypotheses requires detailed comparison of structural features of these families and of Nematocera in general.

Morphological studies of the Deuterophlebiidae are few, with most limited to general descriptions of external characteristics, and little (Edwards 1922; Pulikovsky 1924; Hora 1930) or no (Brodsky 1930; Kitakami 1938; Pennak 1945; Kennedy 1958, 1960) comparative or phylogenetic interpretation. One of the primary objectives of this work is to provide a detailed description of, and standard terms for, cuticular structures of larval Deuterophlebiidae. Although features of the thorax and abdomen are discussed, emphasis is on characteristics of the head and mouthparts. Cranial muscles, which form functional complexes with mouthparts, are also described. Comparison of larval deuterophlebiids with other Nematocera, particularly the Blephariceridae, are included. A phylogenetic analysis of larval features provides a test of the hypothesis of Wood and Borkent (*in press*), specifically testing the monophyly of the Blephariceromorpha, and the relationship between this clade and other Nematocera.

2.3 Materials and Methods

2.3.1 Materials. Larvae of *Deuterophlebia coloradensis* Pennak, *D. inyoensis* Kennedy, *D. nielsoni* Kennedy, *D. shasta* Wirth, *D. sajanica* Jedlicka and Halgos, and three undescribed species (see chapter 4), were examined. Morphological investigations were based mostly on representatives of Nearctic taxa collected during 1984-1987.

Larvae of several other families were examined, including representatives of all instars of the Nearctic blephariceids *Agathon* von Röder, *Bibiocephala* Osten Sacken, *Blepharicera* Macquart, and late-instar larvae of *Philorus* Kellogg. Also examined were larvae of Nymphomyiidae (*Palaeodipteron* Ide), Tanyderidae[1] (*Protanyderus* Handlirsch), Psychodidae (*Maruina* Müller), Tipulidae (*Antocha* Osten Sacken, *Limonia* Meigen, *Hexatoma* Latreille), Ptychopteridae[1] (*Ptychoptera* Meigen), and several Culicomorpha (*Thaumalea* Ruthe[1], *Dixa* Meigen, *Simulium* Latreille[1], *Anopheles* Meigen[1], and several Chironomidae[1]). Specimens and information on larval *Choristella philpotti* Tillyard (Mecoptera: Nannochoristidae) were also available (D.A. Craig, *unpublished data*).

2.3.2 Methods. Specimens were fixed in either 70% ethanol (EtOH) or Carnoy's fluid (3 parts 95% EtOH : 1 part glacial acetic acid), and stored in either 95% EtOH or 70% EtOH. Structural features were determined from whole-animal slide mounts, larval dissections, sections, and scanning electron microscope (SEM) examination.

Most slide-mounted material was cleared in cedarwood oil and mounted in Canada Balsam, generally following procedures of Heming (1969). Variation from his technique included elimination of preliminary steps, since material had been fixed and stored in more concentrated alcohol. Prior to clearing instar III and IV larvae, a small pin was used to puncture cuticle of the ventrolateral prothorax and ventral base of a "middle" and "posterior" abdominal proleg. This, and taking specimens through at least two transfers into pure Cedarwood Oil (the duration of each approximately 2 hours), ensured penetration of the clearing agent. For this technique, specimens fixed in EtOH were superior to Carnoy's-fixed material. The Cedarwood Oil - Canada Balsam method was particularly useful for viewing internal morphological features of the larvae of deuterophlebiids and other Diptera with relatively thin, lightly sclerotized cuticle. Additional material was prepared by removing soft tissues with either lactic acid (Anthon and Lyneborg 1968) or dilute (approximately 10%) potassium hydroxide (KOH). The former were retained in pure lactic acid for viewing, and KOH-treated specimens were either permanently mounted in Euparal, or placed on temporary slide mounts in glycerin or glycerin jelly.

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[1] Early instars (including instar I) also examined.

Specimens fixed in Carnoy's solution were used for sectioning. Standard histological methods (Humason 1979) were followed, with material embedded in paraffin blocks, cut into 6μm sections, and differentially stained with Haematoxylin and Eosin.

Larvae were examined using a WILD M-5 dissecting microscope and a WILD M-20 compound microscope. Observations were recorded with drawings or photomicrographs. Drawings were executed with the aid of either a camera lucida (on M-5) or drawing tube (on M-20), and photomicroscopy with a WILD Camera (MPS 51) and Microphotoautomat (MPS 45), using Kodak Plus-X 35mm film.

Material for SEM examination was prepared by brief (approximately 30 seconds) sonication in EtOH (with 2-3 drops of concentrated ammonia added), followed by critical point drying, and gold-coating in a sputter coater. Prepared material was examined with either a Cambridge Stereoscan 100 or 250 SEM at 10-25kv. Observations were recorded on Kodak Plus-X or Ilford FP4 120mm roll film.

Phylogenetic interpretations and character polarities are based primarily on the classification of Wood and Borkent (*in press*). Their system predicts that the infraorder Tipulomorpha is the sister group of all other Diptera, with the latter clade consisting of four major lineages. The relationships between these four lineages was unresolved. One of these lineages, the infraorder Blephariceromorpha, included the families Nymphomyiidae, Deuterophlebiidae and Blephariceridae, with the Nymphomyiidae hypothesized as the sister group to the latter two families combined. Character polarities are also discussed under the context of the presumed groundplan condition of Diptera (Hennig 1973; Teskey 1981), using Siphonaptera and Mecoptera as primitive outgroups. Unless otherwise indicated, infraordinal names reflect the classification of Wood and Borkent (*loc. cit.*).

2.3.3 Terms for Structures. Descriptions of deuterophlebiids are based primarily on last-instar (IV) larvae, in part because of size considerations, relative development of structures, and a comparatively larger data base (*i.e.*, in the literature) for this semaphoront in other families. However, early-instar larvae were examined, and morphological variations from the final larval stage are indicated. Homologies are based on general resemblance of structures, spatial relationships, and landmark features (*e.g.*, tentorial pits); embryological data were unavailable, though post-hatching ontogenetic information (*e.g.*, histoblast location) was valuable in determining structural homologues. Except for differences discussed below, the descriptive terms of Teskey (1981) are adopted. Terms for musculature are primarily those of Matsuda (1965). Pulikovsky (1924), Brodsky (1930), and Pennak (1945) were useful references for identifying homologous structures in deuterophlebiids.

Terms for structures of the deuterophlebiid cranium are problematic, partly because of unusual features of the dorsomedial and ventromedial head capsule. Depending on larval instar, the dorsal cranium consists of either three separate sclerites (instar I, see Figs. 3, 6) or a single fused sclerite without ecdysial lines (instars II-IV, see Fig. 8). In larval instar I, the medial sclerite approximates a zone normally filled by the frons; however, based on the relative position of certain structures (anterior tentorial pits, frontal ganglion, pharyngeal muscle origins), I refrain from using the term *frons* for this isolated sclerite, and adopt instead, the noncommittal term *frontal sclerite* (*fr*). Additionally, the sclerite apparently contains elements of the occipital carina. Separate cranial sclerites can not be identified in late-instar larvae, and their extent may be approximated only on the basis of other features (*e.g.*, tentorial pits, muscle origins); in most instances, I refer to the region simply as "dorsal cranium".

Another terminological problem pertains to the unusual structure of the ventral head capsule, which consists mostly of membranous cuticle. The genae (*gen*) and prothorax (*pro*) form the respective lateral and posterior boundaries of this zone, with membranous portions of the maxillae (*i.e.*, cardo) delimiting much of the anterior border (see Fig. 10). The remaining anterior boundary consists of the labium (prementum), with which the large membranous zone appears contiguous. According to Snodgrass (1935), the postmentum is that portion of the labium basal or proximal to the prementum, and does not necessarily include sclerotized (*e.g.*, mental, submental, or postmental) plates. I believe the membranous ventromedial part of the deuterophlebiid larval head capsule consists of labial elements, and refer to this area as the *postmentum* (*lmpo*). Adjacent to the postmentum of instar IV larvae is a thick, darkly sclerotized carina (see Figs. 10, 19). This structure forms the ventrolateral margin of the gena, and is named the *postgenal carina* (*pca*). Morphologically, "hypostomal" (*sensu* Snodgrass 1935) carina may a more accurate term, but because of potential confusion with "hypostoma" (*sensu* Teskey 1981, and others), I use the term "postgenal carina".

A relatively detailed description of deuterophlebiid larval mouthparts was given by Brodsky (1930), with more general descriptions provided by Pennak (1945), Kennedy (1958), and others. Most of their interpretations are accepted. Where I discuss features of the larval mouthparts not described in previous papers, homologies are based, in part, on morphology of other families (*cf.* Anthon 1943a; Perraudin 1961; Anthon and Lyneborg 1968).

Systems of chaetotaxy of Diptera are often complex (*e.g.*, larval Culicidae) and sometimes contradictory, and numerous attempts have been made toward simplification (*e.g.*, McAlpine 1981) or standardization (*e.g.*, Saether 1980 for Chironomidae; Harbach and Knight 1980 for Culicidae; Hogue 1978 for Blephariceridae) of terms. According to McAlpine (1981, pg. 10), cuticular outgrowths (hairs, bristles, etc.) should be placed in one of the following categories: (1) macrotrichia (or setae), which are "connected with nerves and are surrounded at the base by a membranous ring or socket"; or (2) microtrichia, which are "superficial extensions of the cuticle". Although his discussion dealt with adult Diptera, similar terms are used for larvae (*e.g.*, Teskey 1981; Saether 1980; Harbach and Knight 1980). This system essentially synonomizes "macrotrichia" and "seta" with several types of hair-like sensilla. Adopting these terms for larval deuterophlebiids would result in confusing and inappropriate naming of cuticular structures; *e.g.*, the extremely long hair-like structures on the lateral margins of abdominal prolegs (see Fig. 38), which are unsocketed and apparently lack innervation, would be called microtrichia under McAlpine's system. According to Snodgrass (1926), a seta is a unicellular external process of the body wall, which is "commonly" (but not always) innervated and surrounded by a membranous socket. Therefore, "seta" is a more general term, applicable to any unicellular cuticular extension, irrespective of the presence of a membranous socket or nervous connections.

An alternate system that conveys information about function has been used for chaetotaxy of larval Blephariceridae (Hogue 1978, 1987) and Chironomidae (Sublette 1979). In Hogue's system, innervated (*i.e.*, socketed) cuticular structures (macrotrichia *sensu* McAlpine 1981) are termed "primary sensilla" if present on larval instar I, and "secondary sensilla" if added in subsequent instars. In Blephariceridae, the latter become quite numerous, often obscuring primary sensilla in later instars (Hogue 1978). Although a small number of sensilla are added in late-instar deuterophlebiid larvae, the above developmental trend is not apparent, and all sensilla of larval instar I can be recognized in later instars. Discussion of deuterophlebiid chaetotaxy will focus on larval instar IV, though no significant differences were observed in earlier instars. I use the term *primary sensilla* for sensilla consistently present in all instars and all taxa examined. Specific names for primary sensilla are based on topographical and positional criteria, and a few are given a numerical designation. Sensilla of the maxillary palps and labial palps are included in respective descriptions of the maxilla and labium; otherwise, all primary sensilla, including those associated with mouthparts, are described only in the section entitled "Chaetotaxy". Secondary sensilla are typically small and present sporadically, and remain unnamed in the present work. The terms *macrotrichia* and *microtrichia* are used for superficial, non-innervated, extensions of the cuticle, with macrotrichia being relatively larger than microtrichia. To alleviate the potential ambiguity of using size boundaries, I attempt to include examples of both macrotrichia and microtrichia where differentiation is necessary.

2.4 Description of Larva

2.4.1 General and Cranium

General (Fig. 1). Body dorsoventrally flattened, broadly convex dorsally, concave ventrally; slightly sclerotized, except head capsule. Head eucephalous, slightly wider than long, dorsoventrally flattened. Antenna elongate, biarticled, with distal article bifurcate. Thoracic segments distinct, separated by lateral incisions (later instars); appendages lacking. Abdomen eight-segmented; segments I-VII with paired, crochet-tipped, lateral prolegs; anal segment (segment VIII) with two tapered, posteriorly directed processes. Anal papillae (*Ap*) of five simple lobes on ventral anal segment. Apneustic.

Dorsal cranium. Instar I: Cranium (Figs. 3, 6) laterally with distinct genae (*gen*); medially membranous, except for elongate frontal sclerite (*fr*). Frontal sclerite posteriorly produced into prothorax; anteriorly with tooth-like egg burster (Figs. 6 (*et*), 7). Dorsal cranium without microtrichia (Fig. 6). Surficial posterior boundary of head and position of entry of frontal sclerite into prothorax marked by small pit posterior to egg burster; pit evident in larval instars II and III, shifted beneath anterior margin of prothorax in instar IV. *Instars II-IV:* Dorsal cranial sclerites fused (Figs. 8, 9), without apparent ecdysial lines; occipital carina markedly developed dorsally, darkly sclerotized, extended into prothorax medially (see also Figs. 16-18). Clypeus with anteromedial margin slightly produced; posterolateral margin forming tentorial phragma (Fig. 2, tph). Dorsal cranium with dense microtrichia (Fig. 8)

Ventral cranium. Instars I-III: Cranium ventromedially with large, membranous, unpigmented postmentum. *Instar IV:* Cranium ventrally (Figs. 10, 19) with membranous postmentum (*lmpo*), delimited laterally by darkly sclerotized, T-shaped, postgenal carina (*pca*). Occipital condyles (*oco*) blunt, projected medially from, and delimiting juncture of, occipital carina and postgenal carina.

Tentorium. Anterior tentorial pits (Figs. 2, 3, 8, 9, *tpa*) distinct, at posterior terminus of tentorial phragma. Tentorial arms unpigmented, uniformly sclerotized; distinction between anterior and posterior arms not apparent. *Posterior tentorial pits: Instars I-III* - pits on membranous cuticle near postmentum-genal boundary; *Instar IV* - pits between occipital condyles and anterior postgenal carina (Fig. 10, *tpp*).

Stemmata (larval eye). Situated posterior to antennal base, arranged in three groups of darkly pigmented cells, two with transparent, ellipsoid lens (Brodsky 1930).

Antenna. Instar I (base labelled in Figs. 3, 6): Antenna with bifurcate distal article, originating from slightly elevated, membranous socket (*ans*); branches of distal article pale, with minute sensilla (see below) on all surfaces; dorsal branch (*and*) tapered toward apex, ventral branch (*anv*) cylindrical and blunt. *Instar II*: Similar to instar I. Proximal article ("basal" article of Pulikovsky (1924), "Schaft" of Brodsky (1930)) minute, unpigmented. *Instar III*: Similar to instar II. Proximal article cylindrical, moderately sclerotized, ca. twice as long as broad; proximal article and antennal socket with sparse microtrichia dorsally.

Instar IV (Fig. 1; base labelled in Figs. 2, 8, 9, 19, 42): Similar to instar III. Proximal article (*anp*) ca. four times longer than broad. Antennal socket (*ans*) with small, sclerotized band posterodorsally; band with three small, circular spots (probably campaniform sensilla) on dorsal margin (Fig. 42, arrowheads).

Antennal sensilla (distal article; Figs. 11-14): (**i**) two blunt, spiniform sensilla on dorsal base of ventral branch (Figs. 11 (*anvs*), 12); grooves evident, multiple pores suggested on some specimens. (**ii**) large, circular, pit-like sensillum (with elevated margins) on ventral branch, anterior to spiniform sensilla; small uniporous peg typically visible within pit (Figs. 11 (*anvp*), 13); may represent a *sensillum coeloconicum*. (**iii**) circular elevations, each with coniform peg (Figs. 11 (*anc*), 14), widely distributed on both branches, but concentrated on ventral apex of ventral branch ("Antennenäste Auswüchsen" of Brodsky 1930); may represent *sensilla styloconica*.

Antennal muscle (Figs. 2, 20, *Mant*). Origin on anterior tentorial arm, insertion on anterior margin of antennal socket.

2.4.2 Mouthparts

Labrum-Epipharynx (Figs. 19, 22, 23). Labrum-epipharynx (*lr*) large, expanded, membranous, extended anteriorly from clypeus, curved ventrally, then posteriorly to cibarium. Torma elongate or broadly triangular, articulated or fused to anterolateral margin of clypeo-labrum, extended posteroventrally toward epipharynx. *Instar I*: Epipharyngeal surface (Fig. 22) densely set with solitary, simple macrotrichia. *Instars II-IV*: Epipharyngeal surface (Figs. 19, 23) with two dense bands of enlarged, spatulate macrotrichia; bands separated anteriorly, converging slightly posteriorly, terminated near near U-shaped epipharyngeal bar (*epb*). Spatulate macrotrichia (Figs. 19, 24, *lrs*) projected medially or ventrally at base, curved laterally at apex; macrotrichia expanded slightly at base, narrow towards middle, expanded and dissected into numerous tines apically (Fig. 25). Lateral epipharyngeal surface with groups of elongate, simple macrotrichia, narrowly united at base. Medial epipharyngeal surface densely set with solitary, simple macrotrichia.

Labral musculature (Figs. 2, 3, 20). Labral retractor of two bundles, with origin on dorsomedial cranium ("frons"), insertion on torma (*M61*) and lateral margin of epipharyngeal bar (*M61'*). Labral depressor (*M63*) origin on clypeus, insertion on medial part of epipharyngeal bar. Intrinsic labral muscle (*Mlr*) laterally extended across clypeolabrum, insertions on tormae slightly dorsad of M61 insertion.

Mandible (Figs. 4, 19, 21-23, 31-33). Mandible predominantly membranous, sclerotized mostly at base and apex. Base darkly sclerotized, ring-like, with thick ventral band, narrow lateral (aboral) bridge, and expanded, moderately sclerotized dorsal band. *Basal mandibular hook* (Figs. 4, 32, 33, ***mdh***) blunt, distally directed, on adoral end of ventral ring. *Prostheca* (Figs. 4, 19, 32, 33, *mdp*) in form of a bundle of several (ca. 20 in larval instar IV) long macrotrichia ("Börstchenpinsel" of Brodsky 1930) slightly dorsad of adoral end of ventral ring; macrotrichia directed toward mouth, covered with apically directed microtrichia. Two small, slightly pigmented, cuticular zones situated dorsad of prosthecal base (on adoral margin). Distal part of mandible mostly membranous, capable of being folded ventrally onto basal part (*i.e.*, toward cibarium). *Mandibular comb* (Figs. 4, 19, 32, 33, *mdc*) at apex of mandible, with 50-60 (instar IV) or fewer (to ca. 20 in instar I) proximally directed teeth along ventral and labral margins; teeth smooth in instar I (Fig. 34), carinate in later instars (Fig. 35). *Subapical mandibular lobe(s)* (Figs. 4, 19, 32, *mdl*) membranous, on labral side of mandible, composed of one prominent lobe and one or two smaller lobes. Mandibular epicondyle anterior to anterior tentorial pit, on tentorial phragma; mandibular hypocondyle anterior to antenna, between lateral mandibular bridge and small, sclerotized, genal lobe.

Mandibular Musculature (Figs. 4, 20-21). Tergo-mandibular (adductor) muscle (*M21*) of four bundles, two each with origin on posterolateral cranium and dorsomedial occipital carina; insertion on large, flat apodeme (*mdad*) attached to ventral ring. Tergo-mandibular (abductor) muscle (*M23*) of two bundles; origin on posterolateral cranium, insertion on narrow apodeme (*mdab*) on aboral margin of dorsal ring.

Maxilla (Figs. 5, 19, 28, 29). Maxilla large, transverse, with inner (adoral) margins in close proximity. Maxilla with membranous *cardo* basally (Fig. 29, *mxc*), and distinct lobes posteriorly (*lacinia*), anteriorly (*galea*), and laterally/aborally (*stipes*). Lacinia (*mxl*) large, thick, predominantly membranous, supported by thin sclerotized rod (Figs. 5, 19, *mxls*); ventromedial margin with crescent-shaped band of macrotrichia, in form of thick, triangular hooks anteriorly, graded to thin, tapered hairs posteriorly; adoral margin with moderately dense, elongate macrotrichia, and several thickened macrotrichia near labium. Lacinia with dark, circular patch (Figs. 5, 19, 29, asterisk) posterior to crescentic band of macrotrichia; possibly of glandular function (see Brodsky 1930). *Stipes* mostly membranous, with small crescent-shaped sclerite laterally (Fig. 5, *mxss*). *Maxillary palp* (Figs. 19, 28, 29, *mxp*) situated on stipes; palp anteriorly with small sclerite (Fig. 5, *mxps*), two campaniform sensilla, and a short hair-like sensillum, apically with 17-18 sensilla (Fig. 30 - homologies based on Craig and Borkent 1980). *Galea* (Fig. 5, 28, 29, *mxg*) mostly membranous, parallel and closely adpressed to anterior margin of lacinia; ventral margin with band of long, thin, adorally directed macrotrichia; apex with small, elongate sclerite (Figs. 5, 19, *mxgs*)

Maxillary Musculature (Figs. 5, 21). Tergo-lacinial muscle (lacinial flexor, *M5*) origin near occipital condyle, insertion basal to lacinial sclerite; stipito-galeal muscle (galeal flexor, *M7*) origin on ventrolateral cranium, insertion on aboral margin of galeal sclerite.

Labium - Hypopharynx (Figs. 19, 26, 27). Labium proximally expanded and membranous (postmentum, *lmpo*), distally bilobed (prementum); prementum typically hidden by adoral margins of maxillae. *Prementum* (*lmpr*) basally with numerous long, anteriorly extended macrotrichia; distal region bilobed, with long macrotrichia on lateral margins; medial margin of each lobe with four prominent conical sensilla, each bearing an apical pit. *Instar I*: labial sensilla closely associated (Fig. 26); *Instars II-IV*: sensilla in two groups, with one near salivary duct opening and a cluster of three (labial palp?, *lmp*) farther ventrad, away from salivary duct (Fig. 27). *Premental sclerites* (Fig. 19, *lms*) paired, small, somewhat triangular, dorsolateral to labial sensilla. *Labial muscle* (Fig. 21, *Mlm*) of two bundles, with origin near occipital condyle, insertion on posterior margin of premental sclerite. *Hypopharynx* (Figs. 19, 26, 27, *hy*) in form of a small lobe between salivary duct opening and cibarium (*cib*), with small, U-shaped sclerite (hypopharyngeal suspensorium); sclerite anteriorly serrate in instar I.

Pharynx apparently simple, without pharyngeal apparatus/filter. *Musculature* (instar IV, Fig. 2): Dilators of cibarium (*M81-82*) of four bundles per side, with origin immediately posterior to anterior tentorial pits, insertion on dorsal cibarium/pharynx. Oral arm retractor (*M74*) of two bundles per side, with origin slightly posterior to M81-82, insertion on pharynx near frontal ganglion (*fg*). Precerebral dilators of pharynx (*M83-85*) with origin on dorsomedial cranium ("frons"), insertion on lateral and dorsolateral pharynx. Postdorsal dilator of pharynx (*M86*) with origin on dorsomedial cranium (posterior "frons"), insertion on dorsal pharynx. Ventral dilators of pharynx (*M87-90*, not figured) with origin on occipital carina (?), insertion on pharynx at level of posterior tentorial pits[1]. Instar I pharyngeal musculature (Fig. 3) similar; M62 and M86 origins on frontal sclerite; other dorsal muscles with origins on membranous cuticle between frontal sclerite and gena; egg burster apparently operated by M86; M74 of two muscle bundles posterolateral to M81-82 and anterior to M83-85 .

2.4.3 Thorax

Thoracic segments dorsoventrally flattened, with round lateral margins. *Instar I*: thorax narrower than head; prothorax indistinct, broadly fused with head capsule (Figs. 3, 6, 15); meso- and metathorax separated by shallow lateral incisions; thorax lacking

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[1] Poor fixation and the delicate nature of these muscles made elucidation of bundles difficult; although several bundles are expected (Matsuda 1965), only 1 was visible in my preparations.

microtrichia. *Instar II*: similar to instar I, but prothorax more distinct (Fig. 16); all segments with sparse microtrichia dorsally. *Instars III-IV*: thorax wider than head, with segments distinct, separated by lateral incisions (Figs. 1, 17, 18); all segments with dense microtrichia dorsally.

2.4.4 Abdomen

Abdomen eight-segmented, with segments IV and V widest (Fig. 1, *aIV*, *aV*). Segments I-VII each with large, eversible, lateral prolegs (pseudopods), bearing rows of crochets distally (Figs. 38, 42). Anal segment (*aA* (segment VIII)) with two tapered, posteriorly directed lobes. Anal papillae (Fig. 1, *Ap*) of five thick, simple, digitiform lobes on ventral side of anal segment, with four lobes ventral, and one dorsomedial, to anus. *Instar I*: dorsal and ventral abdominal surfaces without microtrichia; prolegs each with one row of crochets (Fig. 36). Proleg crochets (Fig. 37) each with 7-8 tines, oriented perpendicular to proleg surface; tines longest basally, progressively shorter distally. *Instar II*: abdomen with sparse microtrichia dorsally, glabrous ventrally; prolegs with elongate macrotrichia on anterior and posterior margins (see Fig. 38, *lpm*). Proleg with three or four[1] rows of crochets; crochets (Fig. 39) basally bifurcate, medially long, thin and keeled, and apically recurved, with five uniformly sized tines oriented parallel to proleg surface. Everted proleg with crochet tines directed laterally or towards base of proleg (Figs. 38, 40); retracted proleg with crochet tines directed distally. *Instar III*: similar to instar II; abdomen with dense microtrichia dorsally (Fig. 38); prolegs each with ca. 7-8 rows of crochets, with number variable between and within individuals - anteroventral and dorsal margins of proleg with greatest and least number of crochet rows, respectively (due to partial rows ventrally). *Instar IV*: similar to instar III; prolegs each with ca. 10-12 rows of crochets.

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[1] Three in *D. nipponica* (Kitakami 1938) and *D. inyoensis* (*personal observation*); four in most other species (*e.g.*, *D. shasta*, *D. nielsoni*, and *D. coloradensis*).

2.4.5 Chaetotaxy

Primary sensilla of a deuterophlebiid larva, as typified by an instar IV *Deuterophlebia shasta* Wirth (Fig. 42), are as follows:

Cranium and Mouthparts:

Anteclypeal sensilla (*ac1-2*) — two sensilla on clypeal margin, anterior to level of mandibular epicondyle; short palmatiform; see also Fig. 9.

Dorsolabral sensilla (*lrd1-4*) — four pairs of sensilla on anterodorsal labrum, between clypeal margin and spatulate macrotrichia; *lrd1* campaniform, *lrd2-4* setiform.

Dorsomandibular sensilla (*dmd1-3*) — three sensilla on dorsum of mandible; *dmd1* campaniform, *dmd2-3* setiform or short palmatiform; see also Figs. 23, 31.

Epicranial sensilla (*ec1-2*)— two sensilla on posterodorsal cranium; *ec1* campaniform, *ec2* short palmatiform, see also Fig. 6.

Galeal sensilla (*gal1-2*)— two sensilla at apex of galea; *gal1* campaniform, *gal2* setiform; see also Figs. 5, 28, 29.

Lacinial sensilla (*lac1-4*) — four sensilla on posterior margin of lacinia; *lac1* short palmatiform, *lac2* "peg-like", *lac3* bifurcate chaetiform, *lac4* setiform; see also Figs. 5, 28.

Median epipharyngeal sensilla (*em1-4*) — four sensilla, linearly arranged from anteromedial labrum to ca. half the distance to epipharyngeal bar; all setiform.

Palatal sensilla (*ep*) — two or three sensilla anterior to lateral margin of epipharyngeal bar; coniform pegs.

Postantennal sensilla (*pa*) — sensillum posterior to antennal base; short palmatiform.

Postclypeal sensilla (*pc1-2*) — two sensilla on clypeal margin, behind level of mandibular epicondyle; *pc1* campaniform, *pc2* short palmatiform; see also Fig. 9.

Postmaxillary sensilla (*pmx1-2*) — two sensilla on anteroventral gena, posterior to maxilla; *pmx1* setiform, *pmx2* bifurcate chaetiform; see also Fig. 23.

Postorbital sensilla (*po1-2*) — two sensilla on posterolateral cranium, behind level of stemmata; short palmatiform.

Subantennal sensilla (*sb*) — four sensilla on ventral cranium, medial to antennal base; three campaniform, one chaetiform or bifurcate chaetiform.

Subgenal sensilla (*sg1-2*) — two campaniform sensilla on ventral gena.

Supraantennal sensilla (*sp1-4*) — four sensilla dorsal to antennal socket and slightly anterior of stemmata; *sp1-3* palmatiform, *sp4* campaniform.

Thoracic (see also Figs. 3, 6):

Laterotergal sensilla (*la*) — lateral-most of major sensilla on dorsum of all segments; lanciform or setiform.

Postlaterotergal sensilla (*pol*) — sensillum posterior or posterolateral to la; setiform or branched setiform.

Prelaterotergal sensilla (*prl*) — sensillum between *sbt* and *la*; setiform or branched setiform.

Subtergal sensilla (*sbt*) — sensillum posterolateral or lateral to *te*; lanciform or setiform.

Tergal sensilla (*te*) — medial-most of major sensilla; lanciform (prothorax) or setiform (meso- and metathorax).

Abdominal (Segments I-VII):

Apical pseudopodal sensilla (*pa*) — apical-most sensillum on dorsum of proleg, near proximal crochet rows; setiform.

Basal pseudopodal sensilla (*pb*) — sensillum on dorsum of proleg base; lanciform.

Medial pseudopodal sensilla (*pm*) — sensillum laterad to *pb*; setiform or branched (segments I-IV), or lanciform (segments V-VII); see also Fig. 38.

Preapical pseudopodal sensilla (*pp1-3*) — group of three sensilla between *pm* and *pa*; *pp1* branched setiform, *pp2* setiform, *pp3* lanciform; see also Fig. 38.

Pseudopodal disc sensilla (*pd*) — (see Figs. 40, 41); two sensilla within proleg disc; chaetiform.

Sternal sensilla (*st*) — sensillum near posteromedial margin of abdominal sternites; chaetiform.

Tergal sensilla (*te*) — medial-most sensillum on dorsum of all segments; lanciform.

Abdominal (Anal Segment):

Apical sensilla (*ap*) — group of sensilla at apex of anal appendage; one long setiform, one short setiform, and two or more digitiform/lanciform sensilla.

Anterotergal sensilla (*at*) — anterior-most sensillum at base of anal appendage, setiform or branched setiform.

Dorsoanal sensilla (*da1-5*) — sensilla along dorsal margin of anal appendage; *da1-2* short palmatiform, *da3-4* setiform and/or branched setiform, *da5* palmatiform.

Mediotergal sensilla (*mt*) — medial-most sensillum at base of anal appendage, setiform or branched setiform.

Posttergal sensilla (*pt*) — posterior-most sensillum at base of anal appendage, lanciform or digitiform.

Thorax and Abdomen:

Intersternal sensilla (*is*) — sensillum near anteromedial margin of thoracic and abdominal (I-VII) sternites; small chaetiform.

Intertergal sensilla (*it*) — sensillum near anteromedial margin of thoracic and abdominal (I-VII and Anal) tergites; small chaetiform.

Laterosternal sensilla (*ls*) — sensillum on ventrolateral margin of thorax and ventral margin of abdominal proleg; small chaetiform.

2.5 Comparative Morphology

2.5.1 Dorsal Cranium. The deuterophlebiid larval cranium is unusual, particularly with respect to structural differences between developmental stages. Homologies of the frontal sclerite of instar I larvae are not entirely clear, and at least two interpretations are possible. First, the frontal sclerite may consist only of elements of the frons, with the anterior margin of the sclerite homologous to the frontoclypeal suture. This arrangement is common to most insects, including the Mecoptera, but typically absent in Diptera (Hennig 1973; Teskey 1981). Among Diptera, bibionid (Teskey 1981) and late-instar blephariceridlarvae (Anthon and Lyneborg 1968) possess a frontal sclerite (frons) delimited anteriorly by a "frontoclypeal" suture. In contrast, instar I larvae of some Blephariceridae (*Agathon*, *Bibiocephala*, *Blepharicera* (*personal observation*)) demonstrate a structure similar to that of deuterophlebiids (*i.e.*, frontal sclerite bordered laterally and anteriorly by apparently membranous cuticle). If the frontal sclerite of instar I deuterophlebiids and blepharicerids consists only of the frons, its anterior margin may be homologous to the frontoclypeal suture of other insects (*e.g.*, Mecoptera). The phylogenetic significance of this interpretation includes the possibility that the Blephariceroidea are the sister group of all other Nematocera, with loss of the frontoclypeal suture a apotypic feature of the latter clade. Considering the paucity of information about early instars (and embryology) of most Nematocera, this interpretation is tenuous, at best. The presence of a "frontoclypeal" suture in Bibionidae, but not in other members of the Bibionomorpha (*sensu* McAlpine, *et al.* 1981), suggests that this feature is not homologous in the Bibionidae and Blephariceroidea.

Hennig (1973) considered absence of a frontoclypeal suture a groundplan feature of Diptera, which is the most parsimonious conclusion under the classification of Wood and Borkent (*in press*). Neither the Nymphomyiidae nor members of the Tipulomorpha possess a frontoclypeal suture, and several features suggest that the isolated frontal sclerite of instar I Deuterophlebiidae and Blephariceridae is secondarily derived and not homologous to the frons of other insects. Firstly, the deuterophlebiid frontal sclerite is apparently a composite structure, including the posteromedial part of the frons and elements of the genae and/or occipital carina. The anterior tentorial pits, frontal ganglion, and pharyngeal muscles, which typically delimit the frons-clypeus border (Snodgrass 1935, 1947), and muscles that normally originate on the frons (M63, M83-85), are associated with membranous cuticle well anterior to the frontal sclerite. Although the sclerite does not encompass the entire frons, certain structures (*e.g.*, egg burster, origin of M86) indicate that the frons is a component of the sclerite. Other structures (*e.g.*, origin of M21) suggest that elements of the gena and occipital carina are also involved. External features (*e.g.*, position of egg burster and anterior tentorial pits) of instar I Blephariceridae suggest a similar arrangement. In larvae of both families, this condition may be the result of desclerotization of the dorsal cranium; alternately, instar I deuterophlebiids and blepharicerids may be developmentally "younger" than most instar I Nematocera (*i.e.*, like precocious embryos), at least with respect to cranial sclerotization. Regardless of mechanism, an isolated frontal sclerite in instar I is unreported for other Nematocera, and may be a synapomorphy of the Blephariceroidea.

Cranial modifications of late-instar deuterophlebiid larvae include fusion of dorsal and lateral sclerites and apparent loss of ecdysial lines (see Fig. 8). These changes have a significant influence on ecdysis. In most eucephalous Diptera, the cranium has distinct regions of thin cuticle (ecdysial lines) that presumably split at ecdysis (Hinton 1963, Hennig 1973). The typical sequence of ecdysis includes initial rupture of the thoracic cuticle and progressive splitting to the head, where the rupture continues at the ecdysial lines (Snodgrass 1947). Absence of ecdysial lines from the cranium of deuterophlebiid larvae requires modified emergence characteristics, with elimination of the final step in a typical sequence. Personal observations of emerging deuterophlebiid pupae and instar IV larvae indicate that, prior to ecdysis, the pharate instar withdraws its head into the thorax of the earlier instar. Subsequently, the thoracic cuticle is ruptured, but, unlike most insects (and Diptera?), the rupture does not continue to the head capsule. The cranium is shed intact, and the functional ecdysial line is actually between the pro- and mesothorax. Comparable cranial structure and emergence behaviour are known for certain Coleoptera and Lepidoptera (Hinton 1963), including some taxa in which early instars possess cranial ecdysial lines that split at ecdysis, but later instars lack these lines and shed an intact head capsule. Ecdysis of instar I and II deuterophlebiid larvae has not been observed, and it is unknown if ecdysial characteristics change with stage of development.

In larval Deuterophlebiidae, the posterodorsal cranial margin is extended medially into the prothorax, in a region where cuticle deposition apparently continues during the intermolt period. This arrangement, which has been reported in relatively few taxa (see below), results in a posterodorsal region of rigid, darkly sclerotized cuticle serving primarily for the origin of mandibular adductor muscles.

In many Blephariceridae (*i.e.*, most members of the subfamily Blepharicerinae), the posterodorsal cranial margin is excised laterally. In contrast, the cranial margin is entire or only slightly excised in the subfamily Edwardsininae and some of the more "primitive" (*sensu* Zwick 1988, *personal communication*) Blepharicerinae (*e.g.*, *Bibiocephala*, some *Agathon*). In these taxa, larval instars I-III demonstrate an unusual cranial modification, in the form of a transverse, posteriorly excised, sclerotized strip. This strip extends posteriorly from the cranial margin to beneath the cephalothoracic cuticle, and has been identified as either a cranial (Tonnoir 1924) or thoracic (Stuckenberg 1958) element. Data for Nearctic blephariceridss[1] confirms Tonnoir's theory about the origin of this sclerotized strip. Examination of larvae at various stages of maturation demonstrates that the sclerotized strip is in fact an extension of the cranium. Furthermore, this cranial extension is apparently deposited during the intermolt period. The increased surface area created by this sclerotized zone accommodates attachment of the large mandibular adductor muscles, which also increase in size during the intermolt period.

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[1] Including *Agathon comstocki*, *A. elegantulus*, and *Bibiocephala grandis*.

Zwick (1977), in his outstanding monograph about Australian Blephariceridae, concluded that "head capsule split posteriorly" was a synapomorphy of the subfamily Blepharicerinae, and implied that the Blephariceridae groundplan included a cranium with an entire posterodorsal margin. This condition appears to be correlated with the presence of intermolt cuticular extensions; thus, the latter may also be a groundplan feature. Interestingly, blepharicerids with pre-existing cranial excisions (*e.g.*, *Blepharicera* sp.) do not demonstrate intermolt cranial extension (though mandibular muscles evidently do undergo some growth (*personal observation*)). Although Zwick's character polarities were based solely on ingroup analysis, similar conclusions may be inferred by outgroup analysis, since the posterodorsal margin of the cranium is entire in the Mecoptera, Siphonaptera, and almost all Nematocera, including Nymphomyiidae.

In addition to Deuterophlebiidae and Blephariceridae, intermolt deposition of cranial cuticle is characteristic of certain Tipulidae (Pritchard 1982; Pritchard and Mutch 1984), and perhaps some Tanyderidae (Anthon 1988). The phylogenetic implications of this pattern are unclear, partly because of the paucity of developmental information about most Diptera. I assume that the apomorphic state has arisen independently in each of the Tipulidae, Blephariceroidea, and Tanyderidae.

2.5.2 Ventral Cranium. Interpretation of the components of the ventral cranium is controversial, with most differences of opinion focussing on the origin of the hypostoma, the anteriorly serrate plate which forms the posteroventral oral margin in larvae of many Nematocera. Although deuterophlebiid larvae lack a hypostoma, resolving the hypostoma controversy may provide insights into homologies of the deuterophlebiid ventral cranium, and character polarities in Nematocera.

Most disagreement pertains to whether or not the hypostoma and post-hypostomal bridge (hereafter called "ventral bridge") are of (1) postgenal (*i.e.*, maxillary segment) origin (Anthon 1943a; Snodgrass 1959; Matsuda 1965); or (2) labial origin (Cook 1949; Gouin 1968; Craig 1969). Inherent in this controversy is a tendency toward recognizing the entire ventral cranium (*i.e.*, hypostoma **and** ventral bridge) as consisting exclusively of labial or postgenal elements. Craig (1969) provided definitive evidence that the simuliid hypostoma is of labial origin, yet Anthon (1943a) presented strong support for a ventral bridge consisting of postgenal elements. Because posterior tentorial pits are a derivative of the maxillary segment (Rempel 1975), their anterior position on the ventral bridge of some Diptera (*e.g.*, Dixidae and Culicidae) provides additional support for a ventral bridge of postgenal origin.

A third option, incorporating aspects of both views, postulates that the hypostoma is a labial (postmental) element and ventral bridge is a postgenal (maxillary) element. Under this hypothesis, the initial stages of hypostomal evolution involved migration of the prementum from the cranial surface to a preoral space, and concurrent anterior movement of the postmentum. This would result in a ventral cranium resembling that of some larval Anisopodidae (*e.g.*, *Obliogaster* (Anthon 1943b)) or Tanyderidae (*e.g.*, *Protanyderus* (*personal observation*; Exner and Craig 1976)), in which the prementum is covered ventrally by an anteriorly toothed hypostoma (postmentum)[1]. Other modifications may include ventromedial expansion or fusion of postgenae to form a ventral cranium like that of many Psychodomorpha (*e.g.*, Psychodidae, Trichoceridae). Fusion of the hypostoma and postgenal bridge is apparent in some families (*e.g.*, Nymphomyiidae (Fig. A.13[2]), Simuliidae, Chironomidae), with a surficial groove typically delimiting the zone of fusion and underlying posterior margin of the prementum or prementohypopharyngeal complex. A similar arrangement is apparent in Tipulidae, although the cranial margin typically bears a ventromedial excision. In many taxa, this excision is extended anteriorly to, or through, the hypostoma, resulting in widely separated genae and a medially divided hypostoma. The latter, therefore, assume the appearance of postgenal lobes, which may account for previous suggestions that the hypostoma is a postgenal element (*e.g.*, Anthon 1943a). The

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[1] Postmentum of *Obliogaster* includes both a mentum and submentum (Anthon 1943b); postmentum of *Protanyderus* refers to the *hypostomium* (*sensu* Exner and Craig 1976).

[2] See Appendix A.

hypostoma may have evolved independently in various nematocerous groups (see below), and its segmental origin could differ between clades; thus, it is possible that the tipulid hypostoma is derived from the maxillary (postgenal) segment. However, morphology of other Nematocera suggests that the tipulid condition reflects fusion of the hypostoma and postgenal bridge in ancestral Tipulidae, followed by ventromedial excision of fused sclerites. Embryological studies will provide a test for these hypotheses.

The presence of widely separated genae, with little or no postgenal contact, is considered plesiomorphic for Diptera (Anthon 1943a; Snodgrass 1959; Hennig 1973; Teskey 1981), but occurs in relatively few taxa (*e.g.*, Anisopodidae). Similar, but presumably analogous, cranial structure occurs in some Tipulidae and Sciaroidea; in these taxa, the presence of a vestigial tentorium suggests further that lack of genal contact is secondarily derived (see below). If a postgenal bridge (and hypostoma) is not part of the Diptera groundplan, the phylogeny of Wood and Borkent (*in press*) suggests that the postgenal bridge (and hypostoma) has either evolved independently or become secondarily lost in most infraorders. The latter is a more acceptable alternative, but raises the question of whether or not a postgenal bridge and hypostoma are groundplan apotypies of Diptera.

It follows that structure of the ventral cranium of Deuterophlebiidae and Blephariceridae presents problems for determining character polarity. In deuterophlebiid larvae, the ventral cranium is predominantly membranous, with no evidence of a sclerotized postgenal bridge. Even in instar IV larvae, which possess a more complete head capsule than early instars, the genae do not meet ventromedially. A similar arrangement is typical of the subfamily Blepharicerinae; in contrast, larvae of the Edwardsininae possess a narrow, sclerotized bridge, thought to be of postgenal origin (Anthon and Lyneborg 1968). Zwick (1977) considered the postgenal bridge a plesiomorphic feature of Blephariceridae. The phylogenetic reconstruction by Wood and Borkent (*loc. cit.*) is consistent with this hypothesis, since the Nymphomyiidae possess a well-developed postgenal bridge. It suggests that lack of a postgenal bridge in larval Blepharicerinae and Deuterophlebiidae is convergent, and due to secondary desclerotization of a previously fused cranium. In deuterophlebiids, the latter is suggested by the position of posterior tentorial pits, which are situated medial to the postgenal carina, in a zone of thin and apparently membranous cuticle. In larvae of most Diptera, the posterior tentorial pits are located on thickly sclerotized cuticle, usually on the postoccipital sulcus (Teskey 1981) or postgenal bridge (*e.g.*, some Culicomorpha). The slightly sclerotized deuterophlebiid tentorium has a minor role in muscle attachment, especially posteriorly, and a rigid ventral cranial contact may be unnecessary. However, the posterior tentorial pits of deuterophlebiid larvae are lateral to the postmentum, a structure which effectively separates the genae. Therefore, desclerotization of the ancestral deuterophlebiid cranium has probably involved the postmentum, rather than a postgenal bridge.

Alternatively, a postgenal bridge may be a synapomorphy of the Edwardsininae, with lack of a bridge a groundplan feature for Blephariceridae. This possibility is indicated by comparing blepharicerids to their hypothesized sister group, the Deuterophlebiidae, and by examining ontogenetic data. In both deuterophlebiids and the Blepharicerinae (Nearctic taxa, *personal observation*), sclerotization of the ventral cranium varies with larval stage, with the distance between sclerotized genal margins greatest in early instars and progressively less with successive molts. It is unknown if the Edwardsininae follow this trend, and examination of early-instar larvae may provide valuable insights into postgenal fusion in these blepharicerids. Instar variability in ventral cranial sclerotization may occur in other groups, but lack of developmental information for most Nematocera (especially for instar I larvae) makes phylogenetic interpretations difficult. For the present, I accept the hypothesis that the Blephariceromorpha groundplan included a postgenal bridge, and that lack of a bridge in the Deuterophlebiidae and certain Blepharicerinae reflects convergent desclerotization of the ventral cranium.

2.5.3 Tentorium. Primitively, the tentorium of dipterous larvae consists of anterior and posterior pits, and well-developed anterior and posterior arms (Anthon 1943a;

Hennig 1973). The plesiomorphic condition, with the posterior tentorial arms extended medially and united to form a posterior bridge, is known only in the Anisopodidae (Keilin and Tate 1940; Anthon 1943a, 1943b), Bibionidae (Perraudin 1961), and Perissommatidae (Colless 1962; Wood and Borkent *in press*). The tentorium, particularly the posterior arms, is reduced in most Nematocera. Larvae of several families, including the Trichoceridae (Keilin and Tate 1940; Anthon 1943a), Ptychopteridae (Anthon 1943a; Kramer 1954), Tanyderidae (*personal observation*), Dixidae (Nowell 1951), Culicidae (Cook 1949), Blephariceridae (Anthon and Lyneborg 1968) and Deuterophlebiidae possess well-developed anterior and posterior arms, but lack a posterior bridge. According to Cutten and Kevan (1970), Nymphomyiidae larvae possess "traces of a tentorial bridge", but their description is difficult to interpret. Light microscopical and SEM examination of late-instar larvae of *Palaeodipteron* confirm the presence of anterior tentorial pits, though tentorial arms and posterior pits are not apparent (*personal observation*). In larvae of most Psychodidae (Anthon 1943a), Chironomoidea (*sensu* Teskey 1981, but see Gouin 1959), Tipulidae (Cook 1949) and Sciaroidea (*sensu* Teskey 1981), the tentorium is vestigial and represented only by posterior tentorial pits.

Reduction or loss of the tentorium is generally coincident with hypostomal development and ventral fusion of the cranium. Ventral closure of the head capsule presumably compensates for tentorial loss by providing increased rigidity and greater cranial surface for muscle attachment (Anthon 1943a; Hennig 1973; Teskey 1981). Exceptions to this trend include the Tipulidae and Sciaroidea, which, despite diversity of cranial development, lack a tentorium. As suggested above, this supports the hypothesis that the partially developed postgenal bridge typical of some lineages is due to secondary desclerotization of a previously fused ventral cranium, rather than retention of the plesiomorphic condition (*i.e.*, lack of a postgenal bridge). Larvae of the Perissommatidae, which possess a well-developed postgenal bridge and relatively complete tentorium (Wood and Borkent *loc. cit.*), are another exception to the general correlation between tentorial reduction and fusion of the ventral cranium. The Deuterophlebiidae also do not fit this pattern. The thin, slightly sclerotized tentorium of a deuterophlebiid larva is of minor importance for muscle attachment, and seems to provide little or no rigidity to the head capsule. Increased sclerotization and rigidity of the dorsal cranium, by fusion of dorsal sclerites into a single contiguous structure, may compensate for lack of rigidity of the ventral cranium. This unusual arrangement could reflect the specialized feeding behaviour and ecology of deuterophlebiids, with the rigid dorsal cranium providing support for mouthpart articulation and musculature, and the membranous ventral surface allowing the head-capsule flexibility needed for collecting diatoms on irregular substrates.

Tentorial reduction apparently has occurred independently in many Diptera, and is therefore not a strong indicator of phylogenetic relationships. The tentorium of larvae of both the Deuterophlebiidae and Blephariceridae resembles that of several other families, many of which are only distantly related. Furthermore, some clades (*e.g.*, Psychodomorpha, Bibionomorpha) demonstrate almost all stages of tentorial development (*i.e.*, from the presumed groundplan condition to a tentorium that is markedly reduced or vestigial), supporting the contention that tentorial characteristics are very homoplastic.

2.5.4 Antenna. One of the most unusual characteristics of larval Deuterophlebiidae is the elongate antenna with a bifurcate distal article. The presence of numerous and varied sensory structures on the distal article, and an apparent haemocoelic continuity with more basal articles, confirm that the distal article represents a true article, and not a pair of modified apical sensilla. Although certain Blephariceridae (*e.g.*, Nearctic representatives of *Agathon*, *Bibiocephala*, *Blepharicera*) possess antennae with forked apical structures, these seem to be modified sensilla rather than true articles (Fig. A.1); the same applies to the enlarged, superficially biramous, apical antennal structures of many other Nematocera larvae, including those of the Nymphomyiidae. I consider the presence of a bifurcate distal antennal article to be an autapomorphy of the Deuterophlebiidae.

The proximal antennal article is relatively elongate in larval Nymphomyiidae and many Blephariceridae, and even more so in the Deuterophlebiidae. Although an elongate larval antenna may represent a synapomorphy of the Blephariceromorpha, the presence of similarly enlarged antennae in other taxa (*e.g.*, Chironomidae), and variation in antennal length in Blephariceridae, indicates the feature may be homoplastic. According to Anthon and Lyneborg (1968), the blepharicerid antenna occupies an unusual position, with the socket having shifted posterolaterally, to well within the genal margin and relatively distant from the frons and peristomal margin. A similar antennal position is suggested in deuterophlebiid larvae. This shift in antennal position would be advantageous for life in torrenticolous habitats, to help maintain a streamlined profile and keep the elongate appendage in lower current velocities of the boundary layer. Although it is possible that this character state has evolved independently in both families, the posterolateral shift of the larval antenna is considered here a synapomorphy of the Blephariceroidea.

In his discussion of the deuterophlebiid larval antenna, Brodsky (1930) reported that "durchgehenden Muskeln" were visible within the "Schaft" (proximal article). The present study has shown that, although the antennal muscle reaches the anterior margin of the socket, it does not extend into the proximal article. Although antennal muscles apparently are lacking from larvae of the Tipulomorpha and Bibionomorpha (both *sensu* Hennig 1973), the groundplan for larval Diptera probably included a single antennal muscle (Hennig 1973) originating from the anterior tentorial arm. The latter are typical of many Nematocera (*e.g.*, see Cook 1949; Félix 1962), including the Deuterophlebiidae and Blephariceridae.

2.5.5 Labrum. The deuterophlebiid labrum is, in many respects, quite generalized; however, several features provide insights into phylogenetic relationships. In larvae of the Nymphomyiidae (Cutten and Kevan 1970), Blephariceridae (*personal observation*; Anthon and Lyneborg 1968), and some Deuterophlebiidae, the torma apparently is articulated (*i.e.*, not fused) to the dorsal labral sclerite, a condition that Wood and Borkent (*in press*) considered a synapomorphy of the Psychodomorpha. If the tormal arrangement in these groups is homologous, it suggests that "torma articulated to the dorsal labral sclerite" may be a constitutive feature at a higher level, supporting the monophyly of the Psychodomorpha + Blephariceromorpha. Other features (see discussion of mandible, below) support this hypothesis.

The ventrolateral surface of the deuterophlebiid labrum-epipharynx bears several rows of enlarged, spatulate macrotrichia (Figs.19, 23-25). These macrotrichia are apparently formed by fusion of several simple macrotrichia, as indicated by basal fusion of macrotrichia on lateral epipharyngeal surfaces. The compound structure of spatulate macrotrichia is suggested further by ontogenetic evidence, since macrotrichia are monomorphic (*i.e.*, simple) in larval instar I, but polymorphic (*i.e.*, simple, simple but fused basally, and spatulate) in later instars. The presence of spatulate or pectinate labral macrotrichia in both Deuterophlebiidae and Nymphomyiidae (Fig. A.14) may indicate common ancestry or, alternatively, suggest that spatulate macrotrichia are part of the Blephariceromorpha groundplan (with secondary loss in the Blephariceridae). However, it seems more likely that that these structures evolved independently in Deuterophlebiidae and Nymphomyiidae.

The intrinsic labral muscle appears to be a deuterophlebiid autapomorphy, probably related to the labrum's massive size and important role in feeding (see below). However, because detailed information about labral musculature is lacking for many Nematocera, it is difficult to state with certainty that homologous muscles are absent from other families.

Unlike deuterophlebiids, blepharicerids possess a laterally compressed, attenuate labrum (Fig. A.2) that seems to play a minor role in feeding. Nonetheless, most labral elements are evident, with structural differences primarily related to size. The "messorial apodeme", "labral retractor muscle", and "labral seta" of Blephariceridae (all *sensu* Anthon and Lyneborg 1968) appear to be homologous to the "epipharyngeal bar", "M61'", and "palatal sensilla", respectively, of Deuterophlebiidae. Unfortunately, these features provide little phylogenetic information, since all are common to most Nematocera and probably represent part of the Diptera groundplan.

A more compelling similarity of the deuterophlebiid and blephariceriid labrum is absence of premandibles (messors). Premandibles occur in most Psychodomorpha (Anthon 1943a; Wood and Borkent *loc. cit.*), Ptychopteromorpha (Anthon 1943a; Exner and Craig 1976), and Culicomorpha (Hennig 1973), yet are rudimentary or lacking in other Nematocera. The "premandibular sclerites" of larval Nymphomyiidae (Cutten and Kevan 1970) are presumably tormae, though adjacent structures could represent premandibles (*e.g.*, medial cluster of pectinate macrotrichia (*personal observation*)); however, the specific homologies of these structures have not been determined. The widespread occurrence of these structures in Nematocera may indicate that premandibles arose early in the evolution of Diptera, possibly as a groundplan feature. Premandibles are markedly developed in most Psychodomorpha, Ptychopteromorpha, and Culicomorpha, and could be a constitutive feature of the three infraorders. If so, absence of premandibles in the Blephariceromorpha raises doubt about a sister-group relationship between this clade and the Psychodomorpha. Possibly the Blephariceromorpha is in fact the sister group of the Psychodomorpha + (Ptychopteromorpha + Culicomorpha); however, the present lack of information on the structure and distribution of premandibles in certain clades (*e.g.*, Bibionomorpha) makes this hypothesis tenuous, at best. Other characters support a sister-group relationship between the Blephariceromorpha and Psychodomorpha; therefore, I assume that the groundplan condition of this clade included well-developed premandibles, and that loss of premandibles is a synapomorphy of the Blephariceromorpha.

2.5.6 Mandible. A general evolutionary trend in larval Nematocera is a shifting of the mandibular rotation from a horizontal, to an oblique, and ultimately a vertical plane (Cook 1949; Schremmer 1951). According to Teskey (1981), this trend reflects a shift in the anterior articulation (epicondyle) to a position higher on the cranium, usually in association with a narrowing of the labrum and cephalic apotome. A developing tentorial phragma may displace further the epicondyle downward and inward, resulting in a nearly vertical mandibular rotation. Condylar displacement and a concomitant oblique to vertical shift in mandibular rotation is typical of larval Psychodomorpha, and some Ptychopteromorpha and Culicomorpha. Wood and Borkent (*in press*) considered this feature a synapomorphy of the three infraorders. A comparable and presumably homologous arrangement occurs in the Blephariceromorpha[1], suggesting that this infraorder and the former three share a common ancestor. The mandibular epicondyle is situated on a tentorial phragma in both the Psychodomorpha and Blephariceromorpha, supporting further the monophyly of these infraorders.

A subdivided ("bisegmented") mandible occurs in larval Ptychopteridae, some Tipulidae, and most Psychodomorpha and orthorrhaphous Brachycera. The mandible of larval Deuterophlebiidae (Figs. 4, 32, 33) consists mostly of membranous cuticle, with sclerotization restricted primarily to the basal ring and apical comb. Thus, the deuterophlebiid mandible may be categorized as "bisegmented". Anthon and Lyneborg (1968) reported that the mandible of a last instar blepharicerid (*Liponeura*) has a "membranous" central area (and thus is subdivided); however, Zwick (1977, pg. 19) argued that the darker (harder) basal strip and mandibular teeth reflect superposition of several sclerotized layers, rather than subdivision (*sensu* Anthon 1943a). Data for Nearctic species suggest that newly molted mandibles do in fact possess a membranous zone; mandibular structure changes dramatically as a larva matures (*cf.* Figs. A.7, A.8), with some modifications perhaps reflecting continuous (intermolt?) sclerotization of the medial zone. Additional information about mandible development is needed to resolve conflicting views about segmentation of blepharicerid mandibles.

Prevalence of subdivided mandibles in presumedly primitive Nematocera has been used as evidence that a subdivided mandible is plesiomorphic in Diptera (Anthon 1943a;

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[1] At present, detailed information about the structure of nymphomyiid mandibles is lacking; mandibular rotation is nearly vertical, but the exact position of the epicondyle is unknown.

Schremmer 1951; Hennig 1973). This hypothesis may support placing Tipulidae, Deuterophlebiidae (and Blephariceridae?), and Psychodomorpha as primitive lineages of Diptera, with undivided mandibles a constitutive feature of the remaining Nematocera. Hennig acknowledged that this hypothesis required a subdivided mandible as a groundplan apomorphy of Diptera, since both the Siphonaptera and Mecoptera possess undivided mandibles. Gouin (1959) considered the subdivided mandible a derived feature of only certain Diptera and, in agreement with Snodgrass (1950), believed that the subdivided condition was due to partial desclerotization. This theory gains support if the subdivided brachyceran mandible is, as suggested by Teskey (1981), secondarily derived and unrelated to the condition in Nematocera. This interpretation seems more acceptable, though partial desclerotization of mandibles may have occurred independently in several lineages. I consider the subdivided mandible a synapomorphy of the Blephariceromorpha + Psychodomorpha. Thus, the structure of the blepharicerid mandible, if unsegmented, would be secondarily derived.

Despite its unique structure, the deuterophlebiid mandible has retained several features of the presumed Diptera groundplan, including the prostheca (a cluster of modified macrotrichia on the adoral mandibular margin). Although absent from larvae of some groups (*e.g.*, Anisopodidae (Anthon 1943a), perhaps Nymphomyiidae (Cutten and Kevan 1970)), a prostheca occurs in most Nematocera, including Blephariceridae. This structure may be homologous to the prostheca of larval Trichoptera (Anthon 1943a) and some Mecoptera ("long setae" at base of "lacinia mobilis" (*sensu* Pilgrim 1972)).

In certain Tipulidae, the prostheca arises from an articulated lobe at the mandible base (Wood and Borkent *loc. cit.*; see Fig. A.9). Wood and Borkent believe this lobe is homologous to the "lacinia mobilis" of Nannochoristidae, and use the character to argue convincingly that the Tipulomorpha is the most plesiomorphic Diptera. Later, they suggest that the "small, subbasal, thumb-like projection" (apparently homologous to the "hakenförmiger Vorsprung ..." of Anthon 1943a) is a synapomorphy of Psychodomorpha.

A similar and probably homologous structure ("basal mandibular hook" *sensu* this paper) occurs in larval Deuterophlebiidae (Figs. 4, 32, 33), and I consider both homologous to the articulated mandibular lobe of Tipulomorpha. This interpretation does not alter the initial dichotomy of Wood and Borkent's phylogeny; *i.e.*, the Tipulomorpha are still the only clade in which the lobe is articulated and bears the prostheca. Rather, it suggests a transformation sequence, in which the basal lobe (or hook) has fused to the mandible base and become reduced in size, with the latter having the secondary effect of shifting the prostheca to the mandible itself. It suggests further that the basal mandibular lobe of most Psychodomorpha and Blephariceromorpha is, in fact, symplesiomorphic. A basal mandibular lobe was not apparent in some blepharicerid larvae (*personal observation*); however, many of these specimens were relatively mature, and mandibular abrasion may have removed any of these structures (*cf.* Figs. A.7, A.8). Mandibles of newly molted larvae possess a rather large basal lobe that may be homologous to the basal mandibular lobe of other taxa. Interestingly, basal lobes occur primarily in taxa with subdivided mandibles; the reason for this correlation is unclear.

Determining the homologies of the deuterophlebiid mandibular comb and subapical mandibular lobe(s) is more difficult. One possibility is that the subapical lobe(s) is a remnant of apical mandibular teeth, and the mandibular comb represents modified "sweeping bristles" ("Fegeborsten" of Anthon 1943a). The latter part of this interpretation is difficult to accept, partly because the deuterophlebiid mandible is, except for the prostheca, devoid of macrotrichia. Furthermore, this hypothesis suggests the possibility that the mandibular comb of the Deuterophlebiidae is homologous to the mandibular comb (*sensu* Wood and Borkent *loc. cit.*) of Ptychopteromorpha + Culicomorpha, which consists of a row of long, curved macrotrichia. Such a homology is doubtful, and it is more likely that both the mandibular comb and subapical lobe(s) of deuterophlebiids are simply modified apical teeth.

Larval Nymphomyiidae also possess a mandible with a multi-toothed, apical comb (Fig. A.14), and this may be a groundplan apomorphy of the Blephariceromorpha. Although the mandible of an instar IV blephariccrid is dramatically different from that of a deuterophlebiid or nymphomyiid (but see Zwick 1977, Fig. 200), those of instar I are quite similar, and support the hypothesis that the Blephariceromorpha groundplan included an apical mandibular comb. In instar I Blepharicerinae (Nearctic taxa), the mandible consists of three lobes, with an apical and medial lobe each terminated in a comb-like series of teeth, and a basal "lobe" consisting of several teeth originating near the prostheca (Figs. A.2-A.4). Teeth are worn rapidly as the instar matures, presumably from abrasion against the substrate during feeding. In late-instar larvae, comb-like lobes are replaced by three large, rigid, straight-edged teeth; this change presumably makes the mandible more robust and abrasion-resistant, thus augmenting its use as a scraping organ.

Alternatively, shared presence of comb-like mandibles may be due to convergence. The mandibles of other taxa, including certain Psychodidae (Feuerborn 1932), bear an apical comb. Structural resemblance could reflect convergent feeding habits, since larvae of all Blephariceromorpha and the above psychodids are grazers. However, I consider the comb-like, larval mandible a synapomorphy of the Blephariceromorpha, and not the result of independent origin in the three constituent families.

2.5.7 Maxilla. The basic structure of the maxilla includes a basal cardo, distal stipes bearing a one-segmented palp, and two endites (galea, lacinia). According to Teskey (1981), most Diptera larvae possess only one recognizable endite, variously identified as the lacinia (Gouin 1959) or galea-lacinia (Matsuda 1965). A general trend toward reduction of the maxilla, particularly involving fusion of endite lobes, is typically associated with increased development of the hypostoma, and the two processes may be related (Gouin 1959). This pattern is consistent in deuterophlebiid larvae, which lack a hypostoma, but possess an enlarged maxilla (Figs. 22, 23) composed of a membranous cardo, well-developed stipes bearing a large maxillary palp, and both endite lobes (lacinia and galea)

(Figs. 5, 19, 28, 29). Larval Blephariceridae also possess an enlarged maxilla with a membranous cardo (Anthon and Lyneborg 1968), and the latter may be a constitutive feature of the Blephariceroidea. Wood and Borkent (*in press*) considered a membranous cardo a synapomorphy of the Psychodomorpha, exclusive of the family Psychodidae. This suggests that a membranous cardo may in fact be a synapomorphy of the Psychodomorpha + Blepharicеromorpha.

2.5.8 Labium. The labium was discussed at length in the section about the ventral cranium, and only a few comments will be added here. The present research has refuted the widely held conclusion (Pulikovsky 1924; Pennak 1945; Kennedy 1958; and others) that the labium is absent from deuterophlebiid larvae. The deuterophlebiid labium consists of an expanded, membranous postmentum and small, bilobed prementum; except for premental sclerites, sclerotized elements are lacking. Although the bilobed condition of the prementum may be plesiomorphic (Anthon 1943a), the deuterophlebiid labium seems rather derived in other respects. Desclerotization of the labium is also evident in larval Blephariceridae, though premental sclerites and a small postmental sclerite are retained in some taxa (Anthon and Lyneborg 1968)[1]. The tendency toward desclerotization of the postmentum, particularly in early instars, may be a synapomorphy of the Blephariceroidea.

2.5.9 Hypopharynx. In larvae of most Nematocera, the hypopharynx is relatively unmodified. The hypopharynx of instar I Deuterophlebiidae is noteworthy, mostly because of its serrate anterior margin (Fig. 26). Similar hypopharyngeal structure is suggested in late-instar larvae of some groups (*e.g.*, Tipulidae (Fig. A.12)), but unknown in first instars. Unfortunately, studies of first instars are few, with most involving certain Culicomorpha. Late-instar Nymphomyiidae possess an anteriorly toothed plate beneath the hypostoma (Fig. A.15), which Cutten and Kevan (1970) called the "lingua of the hypopharynx". If this plate is homologous to the deuterophlebiid hypopharynx, it represents a compelling similarity, perhaps indicative of common ancestry. However, Cutten and Kevan failed to identify the prementum, and I suspect that their "lingua" is actually part of the prementum, rather than the hypopharynx. In some taxa (*e.g.*, Culicomorpha), both may be united into a prementohypopharyngeal complex. If Nymphomyiidae possess a prementohypopharyngeal complex, it raises doubt about their placement in the Blephariceromorpha, since the prementum and hypopharynx are readily distinguishable in Deuterophlebiidae, Blephariceridae and most Nematocera. Until a detailed morphological study can establish definitive homologies for the mouthparts of larval Nymphomyiidae, I interpret the "lingua" as a premental element. Furthermore, the anteriorly serrate hypopharynx of instar I Deuterophlebiidae is considered autapomorphic.

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[1] Examination of blepharicerid larvae in the present study indicates that labial structure of Nearctic species is similar to that of *Liponeura* (Anthon and Lyneborg 1968). However, the postmental sclerite was not apparent in any early-instar (I-III) larvae, and present (but slightly developed) in mature (instar IV) larvae of only a few species (*e.g.*, *Agathon comstocki*).

Although the purpose of the serrate hypopharynx is unclear, it may provide a mechanism for straining food particles from periphytic or detrital mixtures. Instar I deuterophlebiids lack spatulate labral macrotrichia, and possess less-developed mandibular combs and maxillary macrotrichia than later instars. This may result in inefficient collection and processing of food particles, and necessitate a final screening by the hypopharyngeal serrations. In addition, deuterophlebiid eggs may become covered with silt and, upon hatching, instar I larvae may rely on detrital food during their search for suitable habitats. Hypopharyngeal serrations could assist in extracting food particles from detrital mixtures.

2.5.10 Feeding Mechanism. During its forward movement over the substrate, a deuterophlebiid larva continuously moves its head back and forth in an arcing (Wirth 1951) or pendulum-like (Brodsky 1930) motion. This behaviour, which is unique among dipteran grazers, apparently serves to dislodge periphyton. Observations of larval behaviour and mouthpart structure suggest the following feeding mechanism: During the larva's forward movement, the enlarged and modified labrum maintains contact with the substrate and is the primary organ by which food particles are removed. It is responsible for the initial loosening of algae, most of which are probably filamentous diatoms. The mandible then sweeps detached material into the cibarial region, with the ventral teeth of the mandibular comb gathering particles adjacent to the labrum, and teeth on the labral side of the comb cleaning the labral macrotrichia. Abrasion of mandibular comb teeth was evident on some specimens, suggesting that mandibles may remove some algae directly from the substrate; however, their role in this activity is probably minor, compared to the labrum. The enlarged maxilla is equipped with a continuous row of stout macrotrichia on the ventral margin of the lacinia and galea; the maxillae effectively constitute the posterior and partial lateral boundaries of the cibarial cavity. As such, a primary role of the maxilla may be to prevent detached food particles from escaping posteriorly and posterolaterally. Mandibular adduction and concomitant maxillary flexion appear to synchronously direct and concentrate food toward the cibarium. During this action, the stout lacinial macrotrichia may also assist cleaning mandibular comb teeth. The specific role of the deuterophlebiid labium is unknown, though it presumably helps direct food particles into the pharynx.

The feeding mechanism described above, with the enlarged labrum playing a dominant role in feeding, is common to some Nematocera (*e.g.*, Culicomorpha), but rare among dipteran grazers. In most grazing larvae, mandibles are the primary organ of algal removal. Among Blephariceridae, mandibles are important for gathering food, as indicated by rapid abrasion of mandibular teeth during larval growth (*cf.* Figs. A.7, A.8); however, some studies suggest that maxillae play the most active role in feeding (Tonnoir 1930). The large blepharicerid labium bears numerous stout macrotrichia, and may be used to scrape algal material and prevent its escape posteriorly. However, the specific feeding roles of both this organ and the attenuate labrum are unknown.

Morphological differences between the deuterophlebiid and blepharicerid head capsule probably reflect different methods of food acquisition. Although larvae of both families are grazers, a blephariceríd generally restricts its feeding activity to a relatively small area, using its mouthparts to remove periphyton from all layers (*i.e.*, "canopy" to adnate elements). Thus, they are "scrapers" (*sensu* Lamberti, *et al.* 1987). In contrast, deuterophlebiids are essentially "browsers" (*sensu* Lamberti, *et al. loc. cit.*) of the periphytic canopy, feeding over a relatively larger area, but less effective at removing particles to the level of the substrate.

2.5.11 Cephalothorax. Although mountain midge larvae lack a blepharicerid-type cephalothorax (*i.e.*, fused head, thorax, and abdominal segment I (Craig 1967)), the structure of early-instar (I and II) deuterophlebiids suggests a precursor of fused anterior segments. In these life stages, particularly instar I, the head and prothorax consist essentially of a single unit, separable mostly by the position of prothoracic sensilla. In all larval instars, the dorsomedial cranium is extended posteriorly through the prothorax. This tendency toward fusion of anterior segments (or cephalothorax formation) could represent a constitutive feature of the Blephariceroidea.

Morphological differences in the "cephalothorax" of deuterophlebiids and blepharicerids may reflect differences in feeding mechanism (see above) and requirements for head-capsule mobility. In blepharicerids, longitudinal compression of anterior segments has brought previously free segments closer to attachment devices (*i.e.*, ventral suckers), thus allowing larvae to maintain stationary feeding positions on current-exposed substrates. This arrangement is particularly adaptive for blepharicerid larvae, which are relatively robust and expose a large surface area to the current. Larval deuterophlebiids, in contrast, have become dorsoventrally compressed, and their active (*i.e.*, not stationary) feeding behaviour demands more head capsule mobility than in blepharicerids.

2.5.12 Prolegs. Several authors (*e.g.*, Tonnoir 1933; Hora 1930; Craig 1967) have discussed the evolution of ventral suckers in blepharicerid larvae, and others (Hora 1930; Hinton 1955) have evaluated the hypothesis that ventral suckers are homologous to the lateral abdominal prolegs (pseudopods) of deuterophlebiids. These studies have demonstrated convincingly that these structures are not homologous. Only recently (Wood and Borkent *in press*) have discussions considered the possibility that eversible, crochet-tipped, lateral abdominal prolegs in larval Deuterophlebiidae and Blephariceridae (instar I

Blephariceridae (see Figs. A.5, A.6)) are evidence of common ancestry. Zwick (1977) concluded that "eversible hooks on pseudopod" was a synapomorphy of Blepharicerinae, implying it was not part of the Blephariceridae groundplan. It seems more likely that eversible, crochet-tipped prolegs are a constitutive feature at a higher level, providing evidence of monophyly of the Blephariceroidea, and perhaps also the Nymphomyiidae (see Fig. A.17). In fact, Wood and Borkent (*loc. cit.*) defined the Blepharicermorpha on the basis of this character. If these families do constitute a monophyletic group, it is difficult to explain the presence of eversible prolegs as convergence. Even if placement of the Nymphomyiidae in the Blephariceromorpha is equivocal, other evidence indicates that it is more parsimonious to consider the prolegs of the Deuterophlebiidae and Blepharicerinae as homologous. This interpretation is adopted in the present work, with lack of abdominal prolegs in Edwardsininae considered secondarily derived. The function of eversible prolegs in blepharicerids is unknown, but because all larval instars possess well-developed ventral suckers, it is doubtful that prolegs contribute significantly to locomotion or maintenance in torrential habitats. The presence of eversible prolegs in instar I, and loss in subsequent instars, suggests further that prolegs are simply a retained ancestral feature.

2.5.13 Phylogenetic Analysis. Monophyletic groups and proposed phylogenetic relationships (Fig. 43) are based on the following synapomorphic characters (asterisks refer to character states unknown for Nymphomyiidae).

Diptera, exclusive of Tipulomorpha

1* mandible with basal lobe fused to mandible, and prostheca arising directly from median surface of mandible.

Psychodomorpha, Blephariceromorpha, Ptychopteromorpha + Culicomorpha

2 mandibular epicondyle displaced medially and hypocondyle displaced laterally, with mandible rotation oblique to vertical.

Infraorders Psychodomorpha + Blephariceromorpha

3 torma articulated with dorsal labral sclerite.

4* mandible superficially "biarticled", with apex and base separated by a zone of essentially membranous cuticle.

5* mandibular epicondyle situated on tentorial phragma.

6* cardo predominantly membranous.

Infraorder Psychodomorpha

7 premandible in the form of a rounded or oval sclerite with a comb-like row of evenly-spaced, anteriorly projecting teeth — (Wood and Borkent *in press*).

8 labrum laterally compressed, conical or wedge-shaped — (Wood and Borkent *in press*) (convergent with Blephariceridae).

Infraorder Blephariceromorpha

9* loss of premandibles.

10 apex of mandible in form of a multi-toothed comb (at least in instar I).

11 eversible, crochet-tipped, lateral prolegs on abdominal segments I-VII.

12 respiration cuticular, spiracular openings vestigial (*i.e.*, apneustic).

13 anal papillae permanently exerted, nonretractable (see chapter 3).

Superfamily Nymphomyioidea

14 tentorium vestigial, with tentorial arms and posterior tentorial pit not apparent.

15 postmentum (=hypostoma) anteriorly serrate and fused to a postgenal bridge.

16 abdominal prolegs with dimorphic crochets (*i.e.*, simple and pectinate).

17 Malpighian tubules two in number, with both tubules borne on a common stalk originating on the ventral surface of the gut (see chapter 3).

18 ventral surface of labrum-epipharynx bearing several rows of pectinate or spatulate macrotrichia (convergent with Deuterophlebiidae).

Superfamily Blephariceroidea

19* instar I frontal sclerite isolated, separated from clypeus by band of membranous cuticle.

20 antennal socket situated laterally, comparatively distant from peristomal margin.

21 postmentum predominantly membranous, particularly in early instars.

22 posterodorsal margin of cranium laterally excised or medially extended into prothorax, and with a region of intermolt cuticle deposition.

23 head and prothorax indistinguishably fused in early instars (I and II).

24 Malpighian tubules five in number (see chapter 3).

Family Deuterophlebiidae

18 ventral surface of labrum-epipharynx (instars II-IV) bearing several rows of pectinate or spatulate macrotrichia (convergent with Nymphomyiidae).

25 cranium with dorsal and lateral sclerites solidly and indistinguishably fused, lacking ecdysial lines (instars II-IV).

26 distal antennal article bifurcate.

27* labrum partly operated by a fully intrinsic muscle, whose origin and insertion are both situated on labral sclerites.

28* hypopharyngeal suspensorium anteriorly serrate in instar I.

29* loss of pharyngeal apparatus.

30 proleg crochets with five uniformly sized teeth oriented parallel to proleg surface.

31 five anal papillae (see chapter 3).

32 Malpighian tubules terminate in anal papillae (see chapter 3).

33 genae ventromedially separated, not forming a postgenal bridge (convergent with Blephariceridae).

Family Blephariceridae

8 labrum laterally compressed, conical or wedge-shaped (convergent with Psychodomorpha).

11a lateral proleg vestigial on abdominal segment VII, and all prolegs lacking eversible crochets in instars II-IV.

23a head, thorax, and abdominal segment I fused (= cephalothorax) in all instars.

34 cephalic apotome divided by band of membranous cuticle ("frontoclypeal" suture).

35 cephalothorax and abdominal segments II-VI bearing ventral suction devices.

36 tracheal gills on anteroventral margins of abdominal segments II-VI in later-instar (II-IV) larvae.

37 Malpighian tubules borne on a pair of lateral stalks (with a 2+3 or 3+2 arrangement) (see chapter 3).

Subfamily Blepharicerinae

33 genae ventromedially separated, not forming a postgenal bridge (convergent with Deuterophlebiidae).

Subfamily Edwardsininae

11b eversible, crochet-tipped, lateral, abdominal prolegs vestigial in instar I.

2.6 Conclusions

Morphological investigations of Diptera larvae have been invaluable for elucidating phylogenetic relationships, particularly in the Nematocera (*cf.* Wood and Borkent *in press*). As with most families, larvae of the Deuterophlebiidae possess a broad suite of characters — some considered primitive, but many reflecting specialization for life in torrenticolous habitats. Morphological comparison of deuterophlebiids and other Nematocera provides support for: (a) a sister-group relationship between the Deuterophlebiidae and Blephariceridae; (b) a monophyletic Blephariceromorpha composed of the Nymphomyiidae

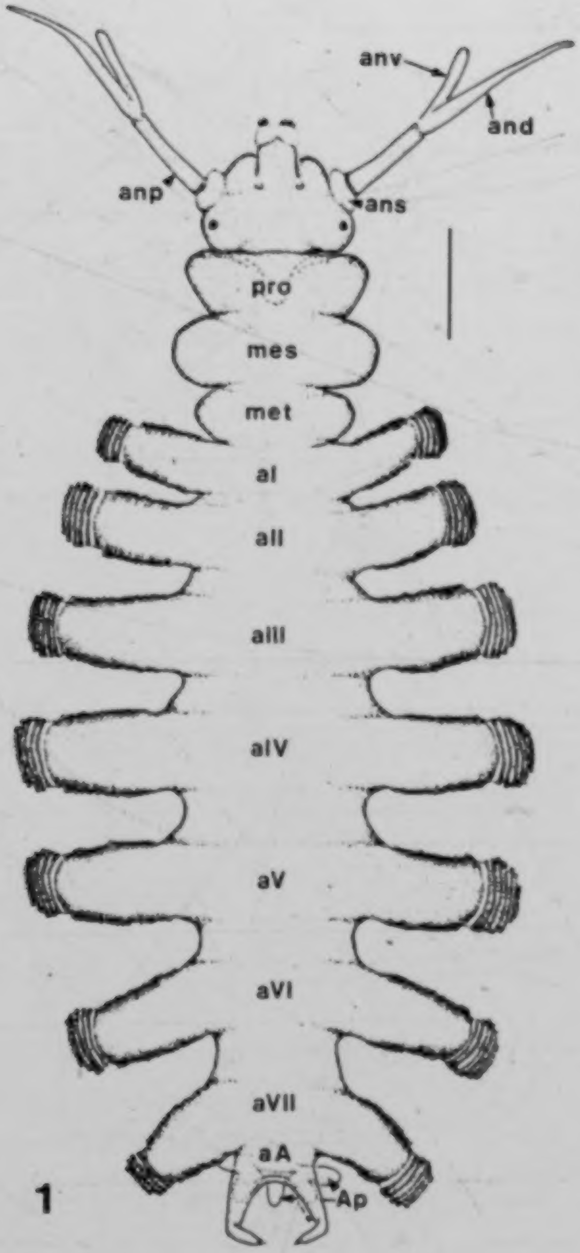
+ (Deuterophlebiidae + Blephariceridae); and (c) a sister-group relationship between the Blephariceromorpha and Psychodomorpha.

The phylogenetic position of the Nymphomyiidae is equivocal, and will remain so until detailed morphological studies are conducted. The eversible, crochet-tipped prolegs of larval Nymphomyiidae provide the most compelling evidence of common ancestry between this family and the Blephariceroidea; however, structure of the larval cranium and mouthparts suggests affinities with other Nematocera, particularly the Culicomorpha. Unfortunately, past attempts to place the Nymphomyiidae, Deuterophlebiidae and Blephariceridae into a phylogenetic system have been confounded by the prevalence of autapomorphic characters. This has invariably led to the conclusion that these families are "primitive" or "archaic", and resulted in their concomitant relegation to near the base of the Diptera. Unravelling this mixture requires detailed morphological studies, with emphasis on features that can be compared across family lines. Definitive conclusions demand comprehensive study of not only larval characters, but features of the pupa and adult. Phylogenetic analysis of all life stages will be the focus of a separate paper (see chapter 3).

It is hoped that this study of larval mountain midges will stimulate and provide a basis for detailed morphological examination of other Nematocera, particularly instar I larvae. Information about the early stages of several families, including Nymphomyiidae, Anisopodidae, Bibionidae, Tanyderidae and Ptychopteridae, will be valuable for deciphering evolutionary trends of Nematocera and establishing a more stable classification of Diptera. In addition, embryological studies are needed to test hypotheses generated in this study and elsewhere. Finally, investigations into behaviour and functional morphology are essential, not only for their descriptive value, but to provide a basis for evaluating mechanisms of evolutionary divergence and convergence.

Figure 1. *Deuterophlebia*, habitus of instar IV larva (dorsal); scale bar = 0.5mm.

Abbreviations: *aI* (to) *VII*, abdominal segments I (to) VII; *aA*, anal abdominal segment; *and*, dorsal branch of distal antennal article; *anp*, proximal antennal article; *ans*, antennal socket; *anv*, ventral branch of distal antennal article; *Ap*, anal papillae; *mes*, mesothorax; *met*, metathorax; *pro*, prothorax.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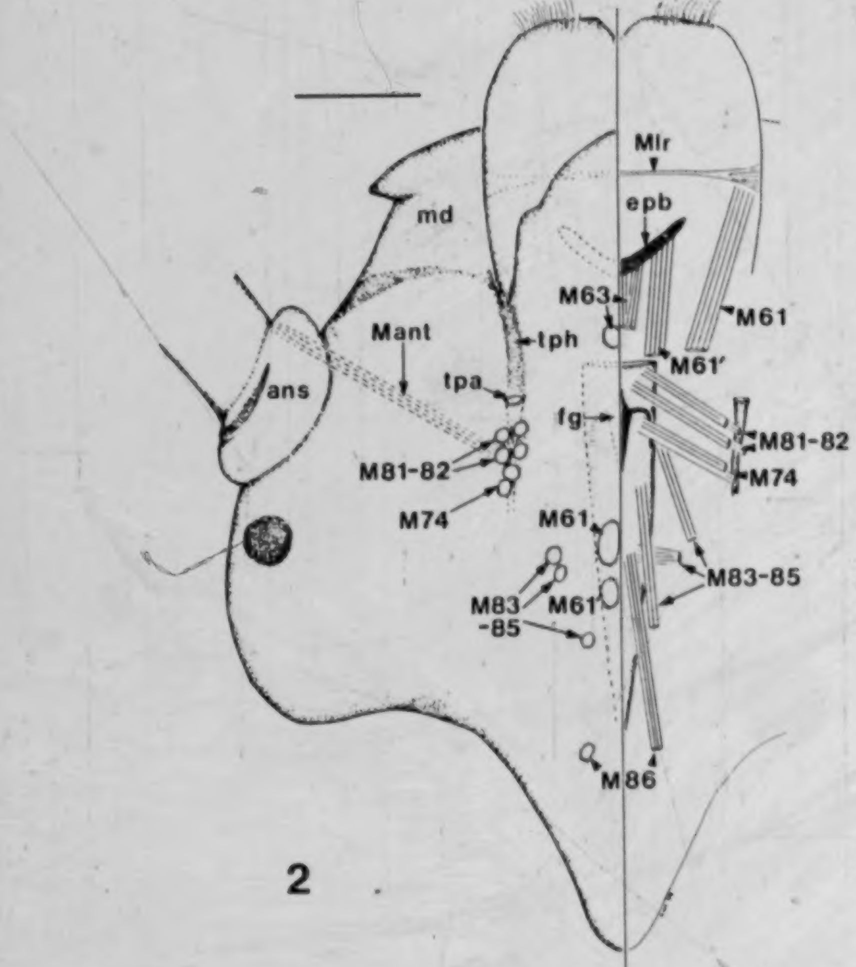
Figures 2-3. *Deuterophlebia*, semi-diagrammatic dorsal view of cranial musculature.

Figure 2. *Deuterophlebia*, head capsule of instar IV larva, showing labral, pharyngeal, and antennal muscles (dorsal view); scale bar = 0.1mm.

Figure 3. *Deuterophlebia*, head capsule and thorax of instar I larva, showing origin of labral and pharyngeal muscles (dorsal view); scale bar = 50μm.

Abbreviations: *and*, dorsal branch of distal antennal article; *ans*, antennal socket; *anv*, ventral branch of distal antennal article; *epb*, epipharyngeal bar; *et*, egg burster; *fg*, frontal ganglion; *fr*, frontal sclerite; *gen*, gena; *M61-61′*, labral retractor; *M63*, labral depressor; *M74*, oral arm retractor; *M81-82*, clypeal dilators of cibarium; *M83-85*, precerebral dilators of pharynx; *M86*, postdorsal dilator of pharynx; *Mant*, antennal muscle; *Mlr*, intrinsic labral muscle; *md*, mandible; *mes*, mesothorax; *met*, metathorax; *pro*, prothorax; *tpa*, anterior tentorial pit; *tph*, tentorial phragma.



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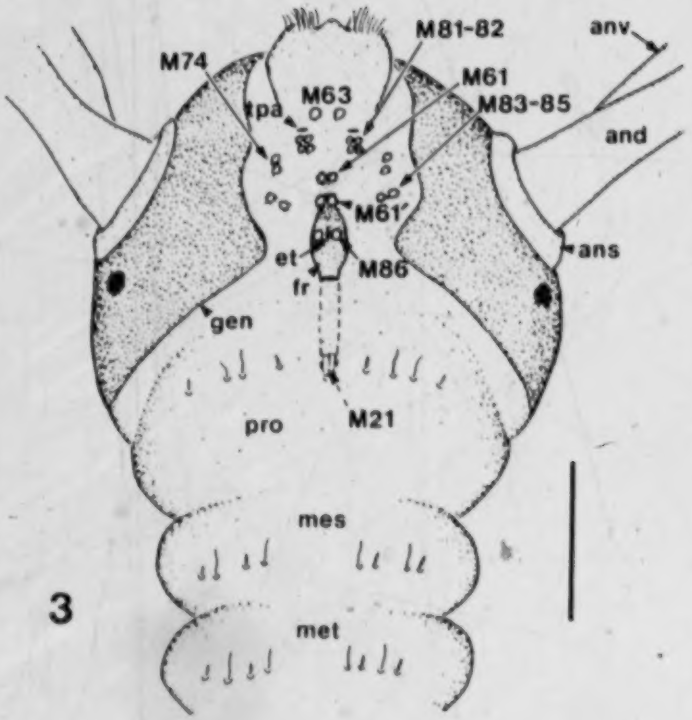

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Figures 4-5. *Deuterophlebia*, mandible, maxilla, and associated musculature of instar IV larva (ventral view); scale bars = 50μm.:

Figure 4. *Deuterophlebia*, larval mandible and mandibular muscles.

Figure 5. *Deuterophlebia*, larval maxilla and maxillary muscles.

Abbreviations: *gal1*, *gal2*, galeal sensilla; *lac1* (to) *4*, lacinial sensilla; *M5*, lacinial flexor; *M7*, galeal flexor; *M21*, mandibular adductor; *M23*, mandibular abductor; *mdab*, apodeme for mandibular abductor; *mdad*, apodeme for mandibular adductor; *mdc*, mandibular comb; *mdh*, basal mandibular hook; *mdl*, subapical mandibular lobe(s); *mdp*, prostheca; *mdv*, ventral mandibular ring; *mxg*, galea; *mxgs*, galeal sclerite; *mxl*, lacinia; *mxls*, lacinial sclerite; *mxps*, maxillary palp sclerite; *mxss*, stipital sclerite; "lacinial patch" indicated by asterisk.

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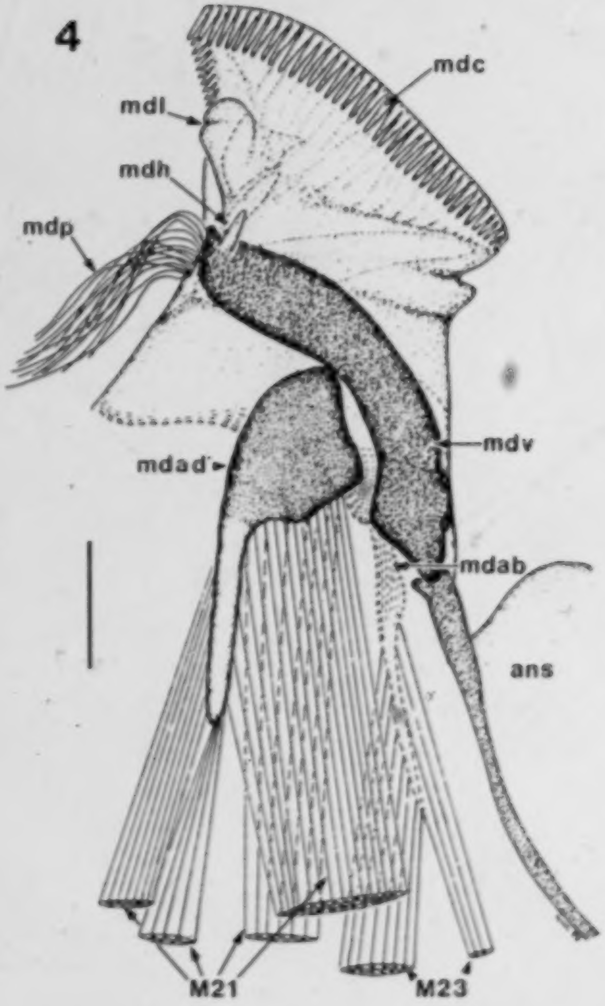
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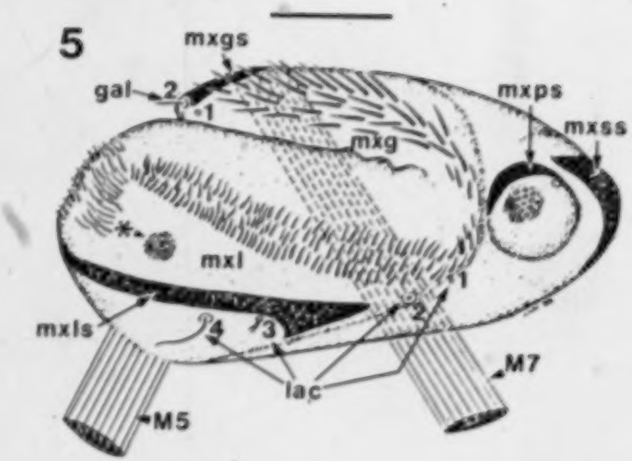
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Figures 6-14. Selected cranial and antennal characters of *Deuterophlebia* larva:

Figure 6. *Deuterophlebia*, head capsule and prothorax of instar I larva (dorsal view); sensilla *prl, sbt, te* (left to right) indicated by arrowheads; scale bar = 50μm.

Figure 7. *Deuterophlebia*, egg burster of instar I larva (dorsolateral view) (anterior = right); scale bar = 3μm.

Figure 8. *Deuterophlebia*, head capsule of instar IV larva (dorsal view); scale bar = 0.1mm.

Figure 9. *Deuterophlebia shasta* Wirth, head capsule of instar IV larva (dorsal view); scale bar = 0.1mm.

Figure 10. *Deuterophlebia*, head capsule of instar IV larva (ventral view of left side); muscle origins (M5, Mlm) indicated by arrowheads; scale bar = 40μm.

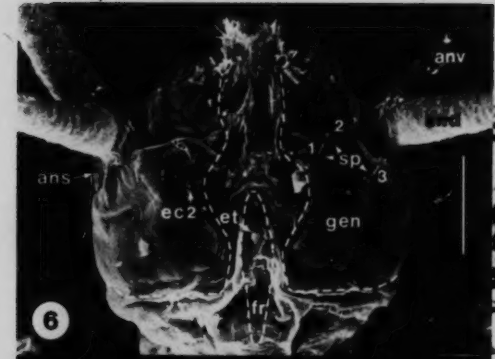
Figure 11. *Deuterophlebia coloradensis* Pennak, base of distal antennal article of instar IV larva (oblique-dorsal view); scale bar = 20μm.

Figure 12. *Deuterophlebia nielsoni* Kennedy, spiniform sensilla on base of ventral branch of distal antennal article (instar IV larva); scale bar = 2μm.

Figure 13. *Deuterophlebia nielsoni*, pit-like sensillum on base of ventral branch of distal antennal article (instar IV larva); scale bar = 4μm.

Figure 14. *Deuterophlebia nielsoni*, coniform sensillum on distal antennal article (instar IV larva); scale bar = 2μm.

Abbreviations: *ac1*, *ac2*, anteclypeal sensilla; *anc*, coniform sensilla; *and*, dorsal branch of distal antennal article; *anp*, proximal antennal article; *ans*, antennal socket; *anv*, ventral branch of distal antennal article; *anvp*, pit-like sensillum; *anvs*, spiniform sensilla; *ec1*, *ec2*, epicranial sensilla; *et*, egg burster; *fr*, frontal sclerite; *gen*, gena; *lmpo*, postmentum; *md*, mandible; *oco*, occipital condyle; *pca*, postgenal carina; *pc1*,*pc2*, postclypeal sensilla; *pro*, prothorax; *sp1* (to) *4*, supraantennal sensilla; *ten*, tentorial arm; *tpa*, anterior tentorial pit; *tpp*, posterior tentorial pit.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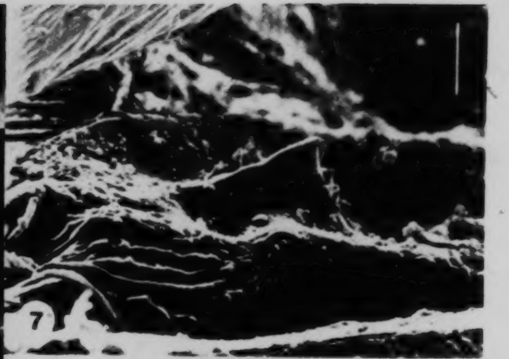
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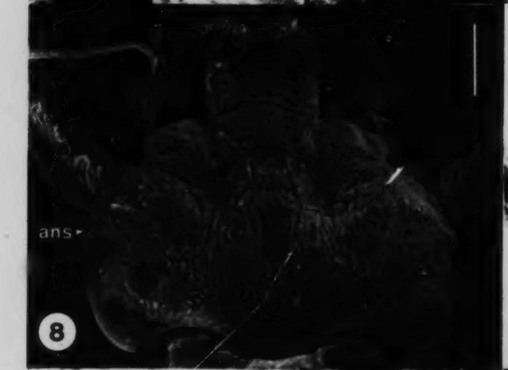
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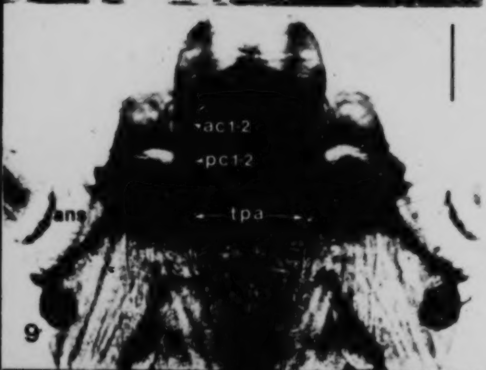
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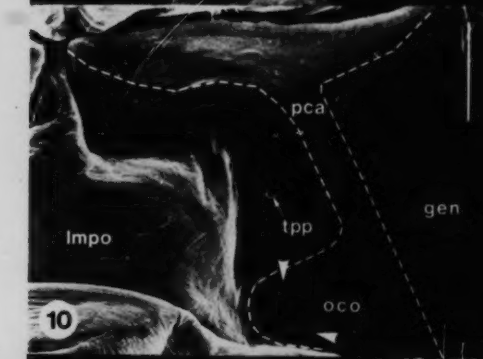
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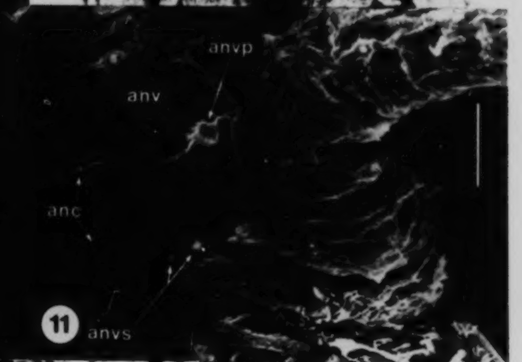
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Figures 15-21. Selected cranial characters of *Deuterophlebia* larva; scale bars = 0.1mm:

Figure 15. *Deuterophlebia*, instar I larva (ventral view).

Figure 16. *Deuterophlebia*, head capsule, thorax, and anterior abdominal segments of instar II larva (ventral view).

Figure 17. *Deuterophlebia*, head capsule of instar III larva (ventral view).

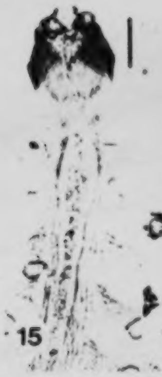
Figure 18. *Deuterophlebia*, head capsule of instar IV larva (ventral view).

Figure 19. *Deuterophlebia*, head capsule of instar IV larva, showing mouthparts (ventral view); "lacinial patch" indicated by asterisk.

Figure 20. *Deuterophlebia*, polarized light photomicrograph, head capsule of instar IV larva, showing labral, pharyngeal, mandibular, and antennal muscles (dorsal view).

Figure 21. *Deuterophlebia*, polarized light photomicrograph, head capsule of instar IV larva, showing mandibular, maxillary, and labial muscles (ventral view).

Abbreviations: *ans*, antennal socket; *epb*, epipharyngeal bar; *ey*, stemmata; *hy*, hypopharynx/hypopharyngeal suspensorium; *lmpo*, postmentum; *lms*, premental sclerite; *lr*, labrum; *lrs*, spatulate labral macrotrichia; *M5*, lacinial flexor; *M7*, galeal flexor; *M21*, mandibular adductor; *M23*, mandibular abductor; *M61-61′*, labral retractor; *M63*, labral depressor; *M74*, oral arm retractor; *M81-82*, clypeal dilators of cibarium; *M83-85*, precerebral dilators of pharynx; *Mlm*, labial retractor; *Mant*, antennal muscle; *md*, mandible; *mdad*, apodeme for mandibular adductor; *mdc*, mandibular comb; *mdl*, subapical mandibular lobe(s); *mdp*, prostheca; *mdv*, ventral mandibular ring; *mx*, maxilla; *mxgs*, galeal sclerite; *mxls*, lacinial sclerite; *mxp*, maxillary palp; *oco*, occipital condyle; *pca*, postgenal carina.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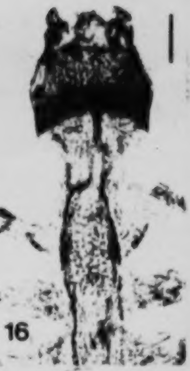
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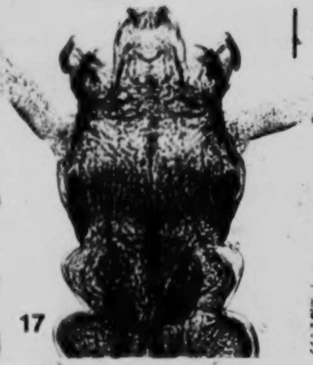
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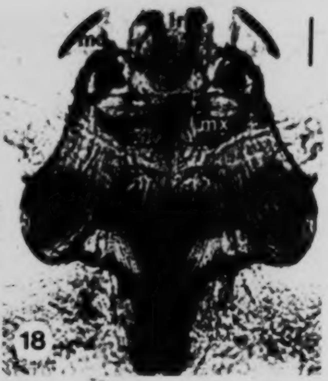
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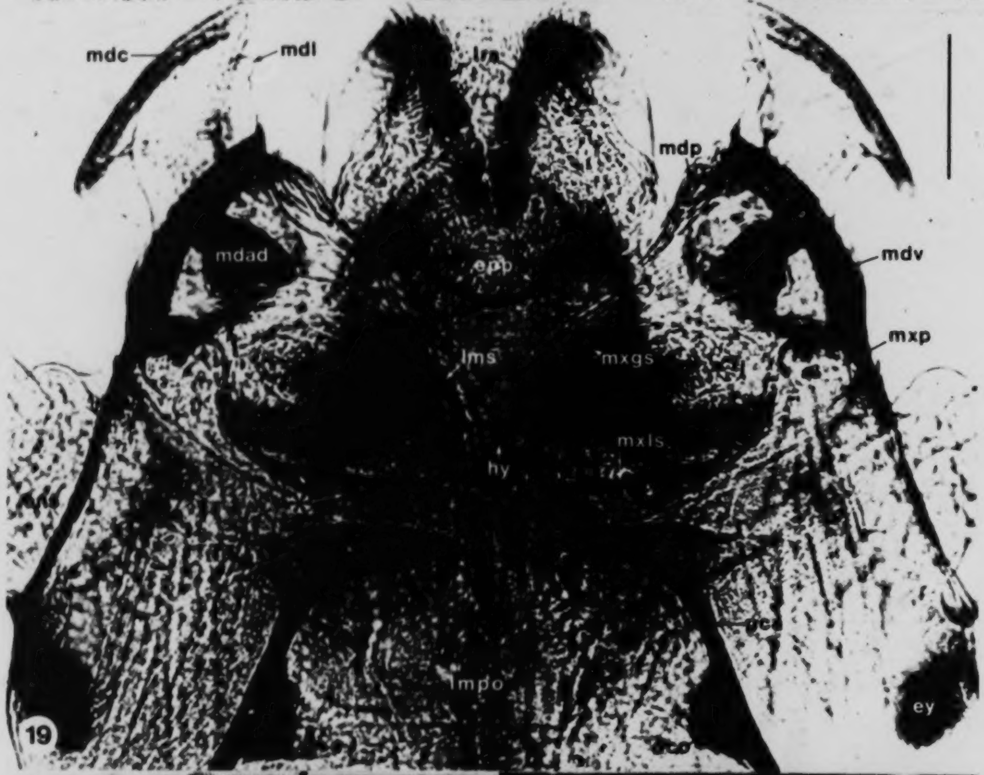
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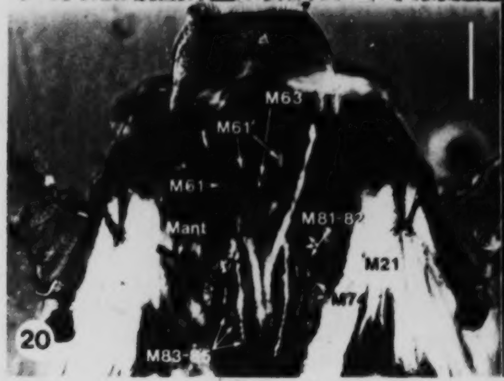
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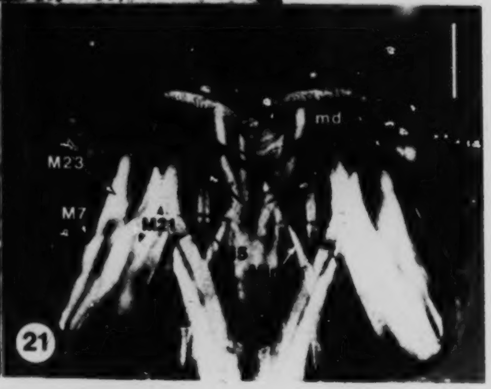
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Figures 22-27. *Deuterophlebia*, larval mouthparts:

Figure 22. *Deuterophlebia*, mouthparts of instar I larva (ventral, to slightly frontal, view); scale bar = 20μm.

Figure 23. *Deuterophlebia*, mouthparts of late-instar (III) larva (ventral view); scale bar = 50μm.

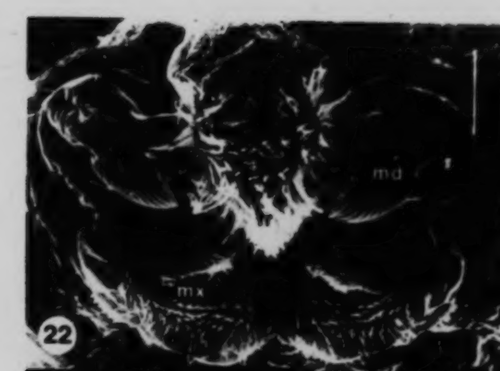
Figure 24. *Deuterophlebia*, labrum of instar IV (dorsal view of left side); scale bar = 5μm.

Figure 25. *Deuterophlebia*, apex of spatulate labral macrotrichia of instar IV larva; scale bar = 3μm.

Figure 26. *Deuterophlebia*, prementum and hypopharynx of instar I larva (ventral view); scale bar = 5μm.

Figure 27. *Deuterophlebia*, prementum and hypopharynx of instar IV larva (ventral view); scale bar = 5μm.

Abbreviations: *cib*, cibarium; *dmd1*, *dmd2*, dorsomandibular sensilla; *hy*, hypopharynx/hypopharyngeal suspensorium; *lmp*, labial palp; *lmpr*, prementum; *lr*, labrum; *lrs*, spatulate labral macrotrichia; *md*, mandible; *mx*, maxilla; *mxg*, galea; *mxl*, lacinia; *pmx1*, postmaxillary sensilla.



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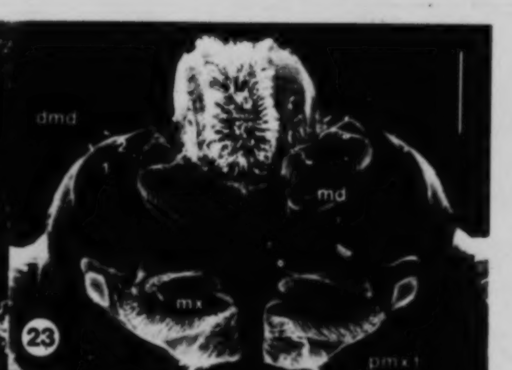

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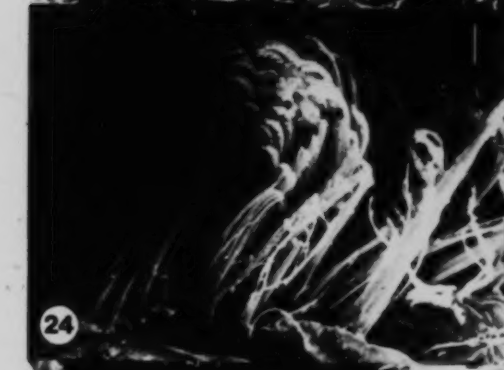

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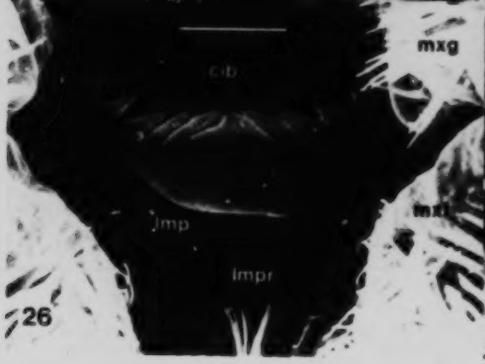

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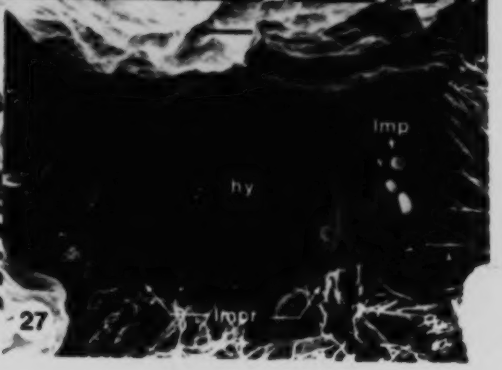

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Figures 28-35. *Deuterophlebia*, larval mouthparts:

Figure 28. *Deuterophlebia*, maxilla of instar I larva (ventral view); scale bar = 10μm.

Figure 29. *Deuterophlebia*, maxilla of instar IV larva (ventral view); "lacinial patch" indicated by asterisk; scale bar = 10μm.

Figure 30. *Deuterophlebia*, maxillary palp of instar IV larva; sensilla notation *sensu* Craig and Borkent (1980); unlabelled sensilla = type "A"; scale bar = 4μm.

Figure 31. *Deuterophlebia*, mandible of instar I larva (aboral view); scale bar = 5μm.

Figure 32. *Deuterophlebia*, mandible of instar IV larva (adoral view); scale bar = 40μm.

Figure 33. *Deuterophlebia*, mandible of instar I larva (adoral view); scale bar = 5μm.

Figure 34. *Deuterophlebia*, mandibular comb teeth of instar I larva; scale bar = 1μm.

Figure 35. *Deuterophlebia*, mandibular comb teeth of instar IV larva; scale bar = 1μm.

Abbreviations: *dmd1* (to) *dmd3*, dorsomandibular sensilla; *gal1*, *gal2*, galeal sensilla; *lac1* (to) *lac4*, lacinial sensilla; *mdc*, mandibular comb; *mdh*, basal mandibular hook; *mdl*, subapical mandibular lobe(s); *mdp*, prostheca; *mxc*, cardo; *mxg*, galea; *mxl*, lacinia; *mxp*, maxillary palp.

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Figures 36-41. *Deuterophlebia*, larval prolegs:

Figure 36. *Deuterophlebia*, proleg of instar I larva (apex); scale bar = 10μm.

Figure 37. *Deuterophlebia*, proleg crochets of instar I larva; scale bar = 4μm.

Figure 38. *Deuterophlebia*, proleg of instar III larva (lateral view); scale bar = 30μm.

Figure 3[illegible]*erophlebia*, proleg crochets of instar IV larva; scale bar = 5μm.

Figure 40. *Deuterophlebia*, everted proleg of instar IV larva (apical view); zone of insertion for proleg retractor muscles indicated by arrowheads; scale bar = 25μm.

Figure 41. *Deuterophlebia*, proleg disc of instar IV larva; organ of unknown function (see text) indicated by asterisk; scale bar = 3μm.

Abbreviations: *lpm*, lateral proleg macrotrichia; *pa*, apical pseudopodal sensilla; *pd*, pseudopodal disc sensilla; *pm*, medial pseudopodal sensilla; *pp1 (to) 3*, preapical pseudopodal sensilla.

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Figure 42. Chaetotaxy of *Deuterophlebia* sp. (based on instar IV of *D. shasta* Wirth); dorsal (left) and ventral (right) perspectives; scale bar = 0.5mm.

Abbreviations: *aI* , *aVII*, abdominal segments I, VII; *ans*, antennal socket; sensilla abbreviations - see Courtney (*in press*), or chapter 2 (pgs. 21-23).

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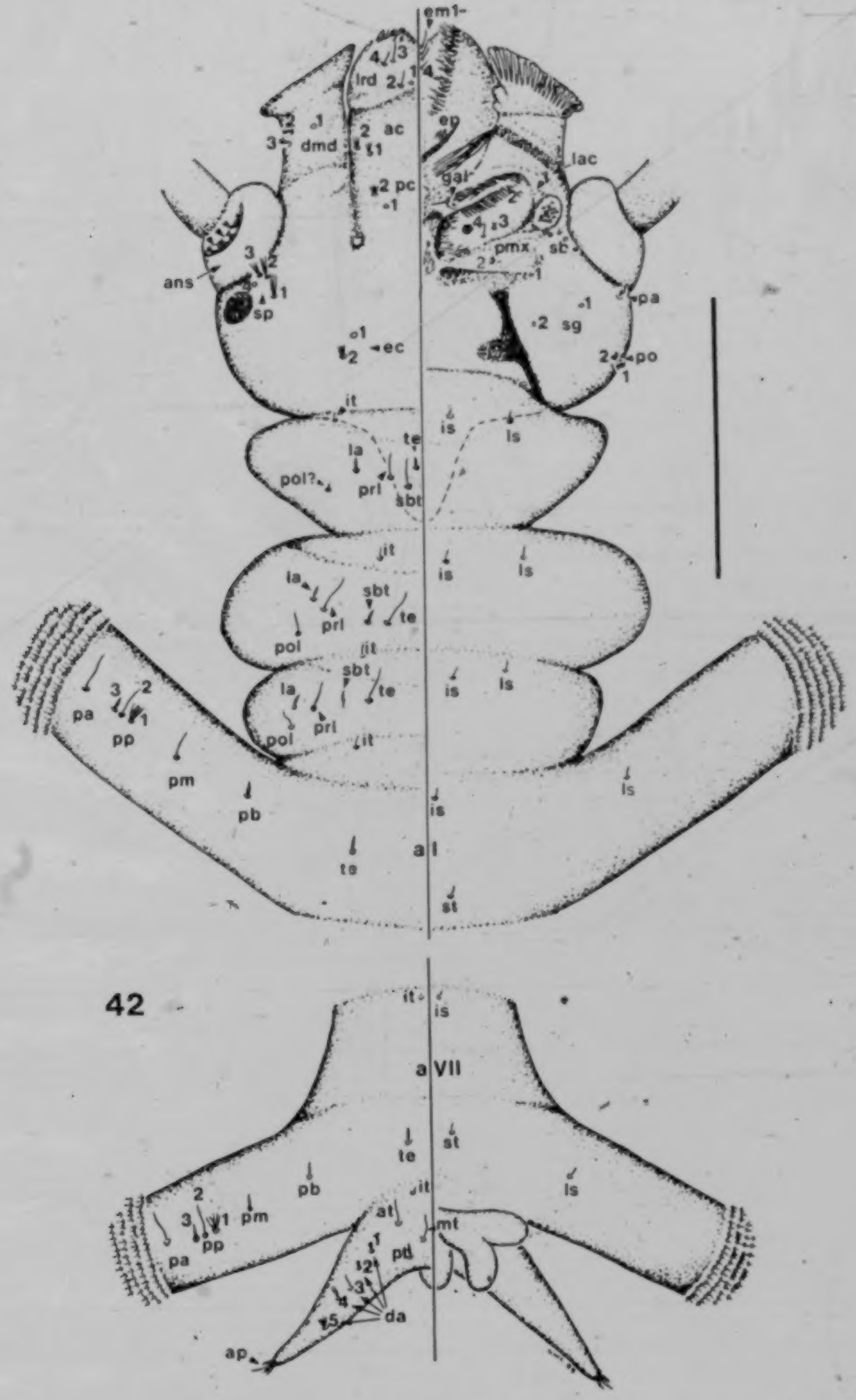
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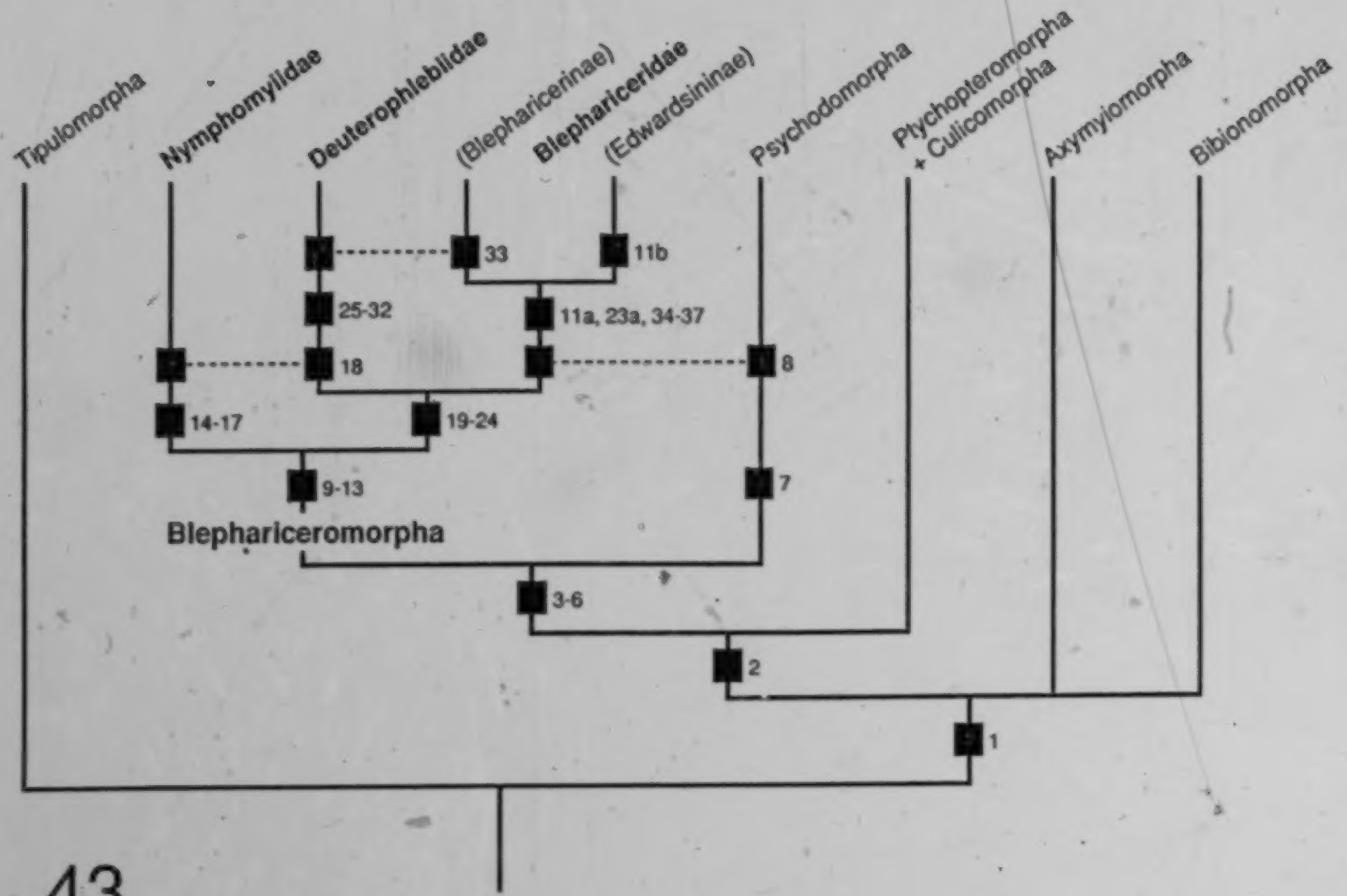
Figure 43. Reconstructed phylogeny of the Blephariceromorpha and related Diptera, based on larval morphology. Apomorphic characters indicated by squares; dashed lines refer to convergences. Relationships of other clades reflect the classification of Wood and Borkent (*in press*).

Apomorphic characters: **1**, basal mandibular lobe fused to mandible, prostheca arising from median surface of mandible; **2**, mandibular condyles displaced, rotation oblique to vertical; **3**, torma articulated with dorsal labral sclerite; **4**, mandible "biarticled"; **5**, mandibular epicondyle on tentorial phragma; **6**, cardo membranous; **7**, premandible a rounded or oval sclerite with comb-like teeth; **8**, labrum laterally compressed; **9**, loss of premandibles; **10**, apex of mandible comb-like; **11**, eversible, crochet-tipped, lateral prolegs on abdominal segments I-VII; **11a**, prolegs vestigial on abdominal segment VII, and prolegs lacking eversible crochets in instars II-IV; **11b**, eversible, crochet-tipped, lateral, abdominal prolegs vestigial in instar I; **12**, apneustic; **13**, anal papillae permanently nonretractable; **14**, tentorium vestigial; **15**, postmentum anteriorly serrate and fused to postgenal bridge; **16**, prolegs with dimorphic crochets; **17**, Malpighian tubules two in number, borne on a common stalk; **18**, labrum-epipharynx with pectinate or spatulate macrotrichia; **19**, instar I frontal sclerite separated from clypeus by membranous cuticle; **20**, antenna lateral, comparatively distant from peristomal margin; **21**, postmentum predominantly membranous; **22**, cranium laterally excised or medially extended into prothorax, with zone of intermolt cuticle deposition; **23**, head and prothorax indistinguishably fused in early instars; **23a**, cephalothorax; **24**, Malpighian tubules five in number; **25**, cranium lacking ecdysial lines; **26**, antenna bifurcate; **27**, labrum partly operated by an intrinsic muscle; **28**, hypopharyngeal suspensorium anteriorly serrate in instar I; **29**, loss of pharyngeal apparatus; **30**, proleg crochets with five uniformly sized teeth; **31**, five anal papillae; **32**, Malpighian tubules terminate in anal papillae; **33**, genae separate, not forming a postgenal bridge; **34**, cephalic apotome divided by membranous cuticle; **35**, cephalothorax and abdominal segments II-VI each with ventral suction devices; **36**, tracheal gills on abdominal segments II-VI; **37**, Malpighian tubules borne on lateral stalks.


Tipulomorpha
Nymphomyiidae
Deuterophlebiidae
(Blephariceriпae)
Blephariceridae
(Edwardsininae)
Psychodomorpha
Ptychopteromorpha
+ Culicomorpha
Axymyiomorpha
Bibionomorpha
33
11b
25-32
11a, 23a, 34-37
18
8
14-17
19-24
9-13
7
Blephariceromorpha
3-6
2
1

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3. PHYLOGENETIC ANALYSIS OF THE BLEPHARICEROMORPHA, WITH SPECIAL REFERENCE TO MOUNTAIN MIDGES (DIPTERA: DEUTEROPHLEBIIDAE).

3.1 Synopsis

Cladistic analysis of the Nymphomyiidae, Deuterophlebiidae, Blephariceridae and related Diptera provides a test of the phylogenetic hypotheses of Rohdendorf (1964, 1974), Hennig (1973), Wood and Borkent (*in press*), and Courtney (*in press 1*). In particular, monophyly of the Blephariceroidea and Blephariceromorpha (both *sensu* Wood and Borkent *loc. cit.*), and their relationship to other Diptera, is tested. Evaluation of larval, pupal and adult characters provides support for the hypothesis of Wood and Borkent (*loc. cit.*), as modified by Courtney (*loc. cit.*). Four larval features suggest the Blephariceromorpha and Psychodomorpha form a monophyletic group. Monophyly of the Blephariceromorpha (Nymphomyioidea + Blephariceroidea) is supported by one adult and five larval characters. Monophyly of the Blephariceroidea (Deuterophlebiidae + Blephariceridae) is supported by 13 synapotypies, including features of the larva, pupa, and adult. Nineteen, 19, and 10 hypothesized synapotypies support the monophyly of each of the Nymphomyiidae, Deuterophlebiidae, and Blephariceridae, respectively.

3.2 Introduction

The nematocerous families Nymphomyiidae, Deuterophlebiidae and Blephariceridae are among the most specialized and distinctive of dipterous insects. The immature stages of all three families are aquatic, and usually associated with torrential mountain streams. Adults are seldom-collected and typically short-lived or cryptic. The Nymphomyiidae contains only five described species: four from the eastern Palaearctic Region (Tokunaga

1932b; Cutten and Kevan 1970; Rohdendorf and Kalugina 1974; Makarchenko 1979), and a single species from eastern North America (Ide 1965). The Deuterophlebiidae contains eight described species, four from each of eastern Asia (Edwards 1922; Kitakami 1938; Jedlicka and Halgos 1981) and western North America (Pennak 1945; Wirth 1951; Kennedy 1958, 1960), and at least six new species from both regions (see chapter 4). The Blephariceridae, with approximately 270 species world-wide (Hogue 1987), is the most diverse and widespread of the three families.

The phylogenetic relationships among the Nymphomyiidae, Deuterophlebiidae and Blephariceridae, and their relationship to other Diptera, has been an enigma. Past attempts to place these families in a phylogenetic system have been confounded by the prevalence of unique, derived (*i.e.*, autapotypic) character states, which has generally led to the conclusion that these taxa are phylogenetically "isolated" and "primitive". Furthermore, life in similar physical conditions (*i.e.*, swiftly-flowing, mountain streams) may have caused substantive morphological convergence (Pulikovsky 1924; Hora 1930; Hogue 1987).

Definitive conclusions about the phylogenetic position of the Nymphomyiidae, Deuterophlebiidae and Blephariceridae requires detailed morphological studies of all life stages, with emphasis on features that can be compared across family lines. The primary objective of this excercise is to use cladistic methods (*sensu* Hennig 1966) to test the phylogenetic hypotheses of Rohdendorf (1964, 1974), Hennig (1973), Wood and Borkent (*in press*), and Courtney (*in press 1*). In particular, I will test for monophyly of the Blephariceromorpha (*sensu* Wood and Borkent *loc. cit.*) and its constituent families, and their relationship to other Diptera. A second goal is to evaluate the hypothesized sister group relationship between the Deuterophlebiidae and Blephariceridae (Wood and Borkent *loc. cit.*; Courtney *loc. cit.*), thus establishing a framework for subsequent phylogenetic analyses of the Deuterophlebiidae (chapter 6).

3.3 History of Classification of Higher Taxa

The Nymphomyiidae, Blephariceridae and Deuterophlebiidae have often been considered primitive lineages of Diptera by various authors (Hennig 1973; Rohdendorf 1964, 1974; McAlpine *et al.* 1981), though few studies have treated in detail the evidence supporting this hypothesis. After detailed morphological studies of *Nymphomyia alba* Tokunaga, Tokunaga (1935, 1936) concluded that the Nymphomyiidae held an archaic and isolated systematic position within the Diptera. This opinion was supported by Rohdendorf (*loc. cit.*), one of few dipterists to place nymphomyiids, deuterophlebiids, and blepharicerids in a comprehensive classification of Diptera (Fig. 1). He recognized five infraorders in the Nematocera: (1) Nymphomyiomorpha; (2) Deuterophlebiomorpha; (3) Blephariceromorpha; (4) Tipulomorpha; and (5) Bibionomorpha. The monobasic infraorder Nymphomyiomorpha was ranked as the most primitive Diptera (suborder "Archidiptera", emended to Archaeodiptera by Kevan and Cutten-Ali-Kahn 1975); subsequently, this interpretation was accepted by several authors (Ide 1965; Cutten and Kevan 1970; Hackman and Väisänen 1982). However, "support" for this hypothesis comes primarily from autapotypic features, or from features that are either homoplastic (*e.g.*, long larval antennae) or of questionable homology (*e.g.*, adult "cerci"). Rohdendorf's (*loc. cit.*) criteria for placing Deuterophlebiidae and Blephariceridae in monobasic higher taxa (infraorders) were, again, either ill-founded or not explicitly stated, with most conclusions pertaining to autapotypies. In all instances, he apparently assumed that extreme specialization was an indicator of early divergence and a long period of evolutionary isolation; in essence, he equated "aberrant" with "plesiotypic".

Hennig (1973) provided the first testable reconstructed phylogeny of Diptera (Fig. 2), using the cladistic methods that he himself formalized (Hennig 1966). Hennig (1973) recognized four infraorders in the Nematocera: (1) Tipulomorpha; (2) Psychodomorpha; (3) Culicomorpha; and (4) Bibionomorpha. He considered the Deuterophlebiidae and Blephariceridae a monophyletic group (superfamily Blephariceroidea), based on similarities in wing folding, development and expansion. He tentatively placed the Blephariceroidea and the monobasic superfamily Nymphomyioidea in the infraorder Psychodomorpha, a group defined by coalescence of the mesomeron and mesoepimeron, an admittedly tenuous synapotypy (Hennig 1973).

McAlpine *et al.* (1981) presented a classification that implied the Nymphomyiidae, Deuterophlebiidae and Blephariceridae form a monophyletic group (infraorder Blephariceromorpha). This hypothesis was recently formalized by Wood and Borkent (*in press*), in a comprehensive phylogenetic analysis of the Nematocera. Wood and Borkent recognized seven infraorders: (1) Tipulomorpha; (2) Blephariceromorpha; (3) Psychodomorpha; (4) Ptychopteromorpha; (5) Culicomorpha; (6) Axymiomorpha; and (7) Bibionomorpha. Wood and Borkent could not resolve the relationships between four major lineages, one of which was the Blephariceromorpha (Fig. 3). Monophyly of the Blephariceromorpha was based on the shared presence of larval abdominal prolegs. An hypothesized sister group relationship between Deuterophlebiidae and Blephariceridae was supported by five characters, including two pupal and three adult features.

3.4 Materials and Methods

3.4.1. Materials. Nymphomyiidae examined for structural features included larvae, pupae and adults of *Palaeodipteron walkeri* Ide. I did not examine representatives of the Palaearctic genera *Nymphomyia* and *Felicitomyia*, so knowledge about their character states comes primarily from the literature (Tokunaga 1935, 1936; Cutten and Kevan 1970; Rohdendorf and Kalugina 1974).

Representative larvae, pupae and adults of all Nearctic and most Palaearctic species of *Deuterophlebia* were examined. Morphological investigations were based primarily on Nearctic taxa collected by the author during 1984-1987. Most examined material was from the author's own collection, and from the collections of various museums (see chapters 2 and 4 for complete listings).

Blephariceridae examined during this study included larvae, pupae, and/or adults of representative *Agathon* von Röder, *Bibiocephala* Osten Sacken, *Blepharicera* Macquart, and *Philorus* Kellogg, *Neucurupira* Lamb, *Elporia* Edwards, *Edwardsina* Alexander, and *Paltostoma* Shiner. Information obtained from specimens was supplemented to a great extent by data from several excellent publications, including Alexander (1958), Anthon and Lyneborg (1968), Hogue (1981, 1987), Stuckenberg (1958), and Zwick (1977).

Although representatives of most nematocerous families were available for study[1], I relied on publications for information about the character states of many taxa (*e.g.*, Axymyiidae, Perissommatidae). Wood and Borkent (*in press*) and various contributed chapters in the *Manual of Nearctic Diptera* (McAlpine *et al.* 1981) were invaluable for this purpose. Several other references (*e.g.*, Crampton 1942; Anthon 1943; Hennig 1973) were also particularly helpful.

3.4.2. Specimen Preparation. Specimens were prepared according to procedures outlined in Courtney (*in press 1*) and Courtney (*in press 2*). When possible, material was examined using a variety of techniques (*e.g.*, whole-animal slide mounts, dissections, sections, scanning electron microscope (SEM)).

3.4.3. Terms for Structures. For most taxa, I follow structural terms outlined in the *Manual of Nearctic Diptera* (*i.e.*, Teskey (1981) for larvae, McAlpine (1981) for adults). Deviations from this system, or new terms specifically applicable to Deuterophlebiidae, are outlined in Courtney (*in press 1*) and Courtney (*in press 2*).

3.4.4. Phylogenetic Methods. Phylogenetic relationships of component taxa of the Blephariceromorpha were determined using cladistic principles *sensu* Hennig (1966). Under this method, common ancestry is determined on the basis of shared, derived, homologous character states, or synapotypies[2]. Similarities reflecting shared, primitive character states (symplesiotypies) or independently derived, non-homologous character states (homoplasies) are rejected. Several comprehensive discussions of cladistic methods are available, including Eldredge and Cracraft (1980), Nelson and Platnick (1981), and Wiley (1981).

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[1] See list provided in chapter 2.

[2] Because this analysis includes both morphological and non-morphological (*e.g.*, ecological, behavioural) characters, I favor the more general suffix "-typy" (Tuomikoski 1967) over the commonly used "-morphy".

One of the major goals, and most difficult tasks, of phylogenetic reconstruction is distinguishing between apotypic, plesiotypic, and homoplastic character states. This task rests, to a large part, on the methods by which polarity decisions are made. When possible, decisions about character polarity (*i.e.*, the direction of character-state evolution) were determined by outgroup methods (Watrous and Wheeler 1981; Maddison, *et al.* 1984). In the present analysis, however, outgroup procedures were confounded by the inadequately resolved phylogenetic relationships among both the taxa of primary interest (Nymphomyiidae, Deuterophlebiidae and Blephariceridae), and between these groups and other Diptera. Although this investigation considers the validity of several phylogenetic hypotheses (in particular, those of Rohdendorf (1974), Hennig (1973), Wood and Borkent (*in press*)), conclusions may be biased by primary use of the classification of Wood and Borkent (*in press*) to polarize characters. This decision is justified, in part, by the fact that Wood and Borkent provide the most comprehensive phylogenetic treatment of Nematocera, to date. As will be evident in pages to come, this does not mean that I whole-heartedly agree with all of Wood and Borkent's polarity decisions or implied character weights. For certain characters, I also discuss polarities in reference to the presumed groundplan condition of Diptera (Hennig 1973; Teskey 1981), using Siphonaptera and Mecoptera as primitive outgroups. Unless otherwise indicated, names for higher taxa reflect the classification of Wood and Borkent (*loc. cit.*).

I have chosen to evaluate a rather large number of characters, certainly more than discussed by Wood and Borkent (*loc. cit.*)[1], and perhaps more than is necessary. I agree with Hecht and Edwards (1977) that "it is better to use fewer well-interpreted morphoclines than to allow obfuscation by mere quantity" (pg. 13); however, at present there are few

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[1] That is, more pertaining to the Blepharicromorpha than discussed by Wood and Borkent.

"well-interpreted morphoclines" among nematocerous Diptera. I discuss numerous characters because of the imprecise resolution of constituent taxa and the prevalence of conflicting characters and apparent homoplasy.

For the most part, I have not adopted a rigorous system of character weighting; however, in accordance with Hecht and Edwards (1976, 1977), I treat synapotypies that are the result of losses or reductions as less reliable than others. This partly explains my acceptance of numerous parallellisms between the Nymphomyiidae and Deuterophlebiidae, most of which presumedly reflect independent loss of structures (*e.g.*, mouthparts, spermathecae) in the short-lived and non-feeding adults. In agreement with Hecht and Edwards (*loc. cit.*) I consider synapotypies involving functional complexes, or unique and novel structures as most informative.

Cladograms were drawn with the aid of software programs available for Macintosh™ microcomputers.

3.5 Monophyletic Groups and Character States

The following discussion of hypothesized monophyletic groups and apotypies is based on characters presented by Wood and Borkent (*in press*), or elucidated by me in the present or earlier (Courtney *in press 1*) analyses. The present analysis deals only with those characters which relate to directly the Blephariceromorpha; *i.e.*, I do not discuss characters which define other higher taxa, unless that taxon includes the Blephariceromorpha as a subordinate taxon.

Each hypothesized monophyletic group is treated individually, but enumeration of characters is consecutive. Character numbers used in the discussion correspond to those in the character matrix (Table 1) and summary cladogram (Fig. 4). For each character, alternate (*i.e.*, hypothesized plesiotypic and apotypic) character states are listed. Several character states have not been determined definitively for the Nymphomyiidae, yet are included in the present analysis; all such characters are indicated by an "(*)", and listed immediately after alternate character states. A brief discussion of character states of potential importance, but undetermined polarity, immediately follows treatments of hypothesized monophyletic groups.

The distribution of character states in nematocerous Diptera is summarized in a character matrix (Table 1). Symbols used in the matrix are as follows[1]: "0" refers to the plesiotypic state; "1" refers to the apotypic state, or the first stage of a hypothesized transformation sequence; "2" and "3" refer to the subsequent stages of any transformation sequence; the presence of multiple character states within a particular taxon is indicated by numbers separated by a slash mark (*e.g.*, "0/1").

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[1] The same notation is used in the discussion of characters, if a transformation sequence is involved.

3.5.1 Diptera, exclusive of Tipulomorpha - Groundplan Apotypies [Larva]

Character 1. *mandible with prostheca arising from articulated basal lobe ("lacinia mobilis"* sensu *Pilgrim 1972) (plesiotypic) / basal mandibular lobe fused to mandible, and prostheca arising directly from median surface of mandible (apotypic)* (*).

The plesiotypic condition occurs in the Nannochoristidae and, among Diptera, only in the Tipulidae (Wood and Borkent *in press*). Wood and Borkent suggest that this lobe is lost entirely in all other Diptera. However, as discussed elsewhere (Courtney *in press 1*), I consider the "small, subbasal, thumb-like projection" (*sensu* Wood and Borkent *loc. cit.*) of Psychodomorpha and the "basal mandibular hook" (*sensu* Courtney *loc. cit.*) of Deuterophlebiidae to be homologous with the articulated mandibular lobe of Tipulomorpha. This suggests the following transformation sequence: (**0**) basal lobe articulated with mandible and bearing the prostheca (*e.g.*, Fig. A.9[1]); (**1**) basal lobe fused to mandible base and reduced in size, with the latter effecting a shift of the prostheca base to the medial margin of mandible (*e.g.*, Figs. 2.32, 2.33); (**2**) basal lobe lost. The mandibular lobe apparently has been lost independently in several lineages, including certain Tipulidae (Fig. A.10), and most or ~~all~~ Ptychopteromorpha (but see Fig. A.11), Culicomorpha, Axymiomorpha, and Bibionomorpha. The same may be true of some Psychodomorpha and Blephariceridae; however, recent data about Nearctic Blepharicerinae (see Courtney *in press 1*) suggest that larval blephariceridae possess a basal lobe, but it is abraded rapidly through feeding activities.

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[1] See Appendix A.

3.5.2 Psychodomorpha, Blephariceromorpha, Ptychopteromorpha, and Culicomorpha - Groundplan Apotypies [Larva]

Character 2. *mandibular condyles located more or less dorsoventral to each other, with mandible rotation horizontal (plesiotypic) / mandibular epicondyle displaced medially and hypocondyle displaced laterally, with mandible rotation oblique to vertical (apotypic).*

According to Wood and Borkent (*in press*), the plesiotypic condition occurs in all outgroups of Diptera (Siphonaptera and Mecoptera) and, among nematocerous groups, in the Tipulomorpha, Axymiomorpha, and Bibionomorpha. Condylar displacement and a concomitant oblique to vertical shift in mandibular rotation is characteristic of larval Psychodomorpha, and some Ptychopteromorpha and Culicomorpha. Wood and Borkent (*loc. cit.*) considered this feature a synapotypy of the latter three infraorders. As discussed elsewhere (Courtney *in press 1*), a comparable and possibly homologous arrangement occurs in Blephariceromorpha, indicating that this clade and the former three form a monophyletic group. However, I accept this synapotypy with some reservation, partly because several members of the Ptychopteromorpha and Culicomorpha, as well as a few Psychodomorpha, demonstrate the plesiotypic condition (*i.e.*, mandible rotation horizontal). Wood and Borkent (*loc. cit.*) interpreted the horizontal mandibular rotation in these groups as reversals due to larval habitat and feeding behaviour. However, all of this suggests that the character may be subject to homoplasy and, therefore, of questionable value in phylogenetic interpretations. The Brachycera, or the so-called "higher" flies, also demonstrate vertical mandibular rotation, and further insights about the phylogenetic value of this character may be gained by elucidating the phylogenetic relationship between these flies and the Nematocera.

3.5.3 Psychodomorpha and Blephariceromorpha - Groundplan Apotypies [Larva]

Character 3. *torma fused with dorsal labral sclerite (plesiotypic) / torma articulated with dorsal labral sclerite (apotypic).*

The torma of larval Nymphomyiidae (Cutten and Kevan 1970), Blephariceridae (*personal observation*; Anthon and Lyneborg 1968), and some Deuterophlebiidae apparently is articulated to the dorsal labral sclerite. I consider this arrangement homologous to that of the Psychodomorpha (Wood and Borkent *in press*), supporting monophyly of the Psychodomorpha + Blephariceromorpha. The torma is also articulated to the labrum in the Culicomorpha, and this condition may in fact be a synapotypy of the Ptychopteromorpha, Culicomorpha, Psychodomorpha and Blephariceromorpha. However, I concur with Wood and Borkent's interpretation that the culicomorph arrangement is not homologous to that of the Psychodomorpha (and Blephariceromorpha).

Character 4. *mandible more or less uniformly sclerotized, with apex and base solidly fused (plesiotypic) / mandible superficially biarticled, with apex and base separated by a zone of essentially membranous cuticle (apotypic)* (*).

The plesiotypic state is characteristic of all outgroups of Diptera (*e.g.*, Siphonaptera, Mecoptera) and, among Nematocera, of the Culicomorpha, Axymiomorpha, Bibionomorpha, and most Tipulomorpha and Ptychopteromorpha. Superficially biarticled (subdivided) mandibles are found in larvae of most Psychodomorpha, and all Deuterophlebiidae and, perhaps, Nymphomyiidae (Courtney *in press 1*). The apotypic state presumably reflects partial desclerotization of the medial portion of the mandible. Although the biarticled mandible may have evolved independently in these lineages, it is more parsimonious to consider this condition as homologous; therefore, it may represent a synapotypy of the Psychodomorpha + Blephariceromorpha. This interpretation requires that the apparently unsegmented mandible of larval Blephariceridae[1] reflects secondary sclerotization. Biarticled mandibles also occur in larval Ptychopteridae, some Tipulidae, and in orthorrhaphous Brachycera; this condition, at least in the former two groups, is probably not homologous to that of the Psychodomorpha + Blephariceromorpha.

Character 5. *mandibular epicondyle situated at anterior end of tentorial arm, near anterior junction of genae and frontoclypeal apotome (plesiotypic) / mandibular epicondyle situated on tentorial phragma (apotypic)* (*).

A shift in the mandibular rotation from a horizontal to an oblique or vertical plane (see character 2) reflects a shift in the anterior articulation (epicondyle) to a position higher on the cranium, usually in association with a narrowing of the labrum and cephalic apotome (Teskey 1981). A tentorial phragma may further displace the epicondyle downward and inward, resulting in a nearly vertical mandibular rotation. The mandibular epicondyle is situated on a tentorial phragma in both the Psychodomorpha and Blephariceromorpha, providing further support for monophyly of these two infraorders. A similar, and possibly homologous, arrangement is found in all orthorrhaphous Brachycera.

Character 6. *cardo represented, in part, by a clearly delineated sclerite (plesiotypic) / cardo predominantly membranous (apotypic)* (*)

Wood and Borkent (*in press*) considered a membranous cardo a synapotypy of the Psychodomorpha, exclusive of the family Psychodidae. Larvae of both the Deuterophlebiidae and Blephariceridae possess an enlarged maxilla with a membranous cardo. It seems likely that a membranous cardo is in fact a synapotypy of the Psychodomorpha + Blephariceromorpha.

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[1] Although Zwick (1977) contends that the blephariceríd mandible is not biarticled, it seems that newly molted mandibles of many Nearctic species in fact do possess a distinct membranous zone (*personal observation*); as the larva matures, several changes in mandibular structure are evident (*cf.* Figs. A.7, A.8), including increased sclerotization of this zone. See also chapter 2.

3.5.4 Psychodomorpha - Groundplan Apotypies [Larva]

Character 7. *premandible in the form of a simple, small, unadorned sclerite, serving only as the point of insertion of the labral retractor muscles (plesiotypic) / premandible in the form of a rounded or oval sclerite with a comb-like row of evenly-spaced, anteriorly projecting teeth (apotypic)* — (Wood and Borkent *in press*).

I concur with Wood and Borkent's contention that the structure of the Psychodomorph premandible is one of the more convincing synapotypies of the infraorder. Larvae of the Blephariceromorpha apparently lack premandibles, presumably because of secondary loss (see character 9); alternate hypotheses are given elsewhere (Courtney *in press 1*).

Character 8. *labrum dorsoventrally flattened (plesiotypic) / labrum laterally compressed, conical or wedge-shaped (apotypic).*

The plesiotypic state is found in the Mecoptera and most Nematocera, including the Tipulomorpha, Ptychopteromorpha, Bibionomorpha, and most Culicomorpha. It is also characteristic of the blephariceromorph families Deuterophlebiidae and Nymphomyiidae. The apotypic state occurs, presumably by convergence, in the Axymiomorpha (Mamayev and Krivosheina 1966), Thaumaleidae, Blephariceridae, and most Psychodomorpha (Wood and Borkent *in press*).

3.5.5 Blephariceromorpha - Groundplan Apotypies

3.5.5.1 Larva

Character 9. *premandibles in the form of either a small, simple sclerite, or an oval sclerite bearing a comb-like row of teeth (plesiotypic) / premandibles absent (apotypic)* (*).

Premandibles apparently are lacking from the larvae of all Blephariceromorpha[1]. Well-developed premandibles are characteristic of most Psychodomorpha (Anthon 1943; Wood and Borkent *loc. cit.*), Ptychopteromorpha (Anthon 1943, 1988), and Culicomorpha (Hennig 1973); these labral structures are indistinct but apparently present in other Nematocera (Wood 1989, *personal communication*)[2]. As discussed elsewhere (Courtney *in press 1*), markedly developed premandibles may be a constitutive feature of the Psychodomorpha, Ptychopteromorpha, and Culicomorpha. If so, the absence of premandibles from Blephariceromorpha raises doubt about a sister-group relationship between the Blephariceromorpha and Psychodomorpha. The Blephariceromorpha in fact could be the sister group of the Psychodomorpha + (Ptychopteromorpha + Culicomorpha); however, the present lack of knowledge about the premandibles of certain groups (*e.g.*, Bibionomorpha) makes this hypothesis tenuous. Other characters support a sister-group relationship between the Blephariceromorpha and Psychodomorpha. Therefore, I assume the Psychodomorpha + Blephariceromorpha groundplan included well-developed premandibles and that absence of premandibles in Blephariceromorpha is a secondary loss.

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[1] As discussed elsewhere (Courtney *in press*), knowledge about the larval mouthparts of Nymphomyiidae is presently inadequate; until more information about labral structure is available, definitive statements about the presence and/or structure of nymphomyiid premandibles are not possible.

[2] According to Wood and Borkent (*loc. cit.*), premandibles are rudimentary in Thaumaleidae, and lacking from Chaoboridae and Corethrellidae.

Character 10. *apex of mandible bearing only a few stout teeth, without apical comb (plesiotypic) / apex of mandible in the form of a multi-toothed comb (at least in instar I) (apotypic).*

The larval mandibles of both the Deuterophlebiidae and Nymphomyiidae bear a multi-toothed, apical comb, consisting of a row of several, more or less uniformly sized teeth[1]. Mandibles of instar I Blephariceridae are rather similar, including three lobes, with the apical two terminating in a comb-like series of teeth (Figs. A.2-A.4). In late-instar larvae of most blephariccrids, the three comb-like lobes are replaced by three rigid, straight-edged teeth (Fig. A.7), a change that presumably makes the mandible a more effective scraping organ. Comb-like mandibles occur in a few other taxa (*e.g.*, Psychodidae - *Maruina* (Feuerborn 1932)) with similar feeding habits (*i.e.*, grazing), and structural resemblance of deuterophlebiid, nymphomyiid, and blepharicerid mandibles may reflect convergence. However, most nematocerous grazers (*e.g.*, Thaumaleidae; Simuliidae - *Gymnopais* Stone) demonstrate the plesiotypic state. Because all members of the Blephariceromorpha possess an apical mandibular comb, at least in the first instar, I consider this feature a synapotypy of the infraorder, rather than the result of independent origin in the three constituent families.

Character 11. *abdominal segments I-VII without lateral prolegs (plesiotypic) / abdominal segments I-VII each with a pair of elongate, eversible, crochet-tipped, lateral prolegs (apotypic).*

All larval instars of the Nymphomyiidae and Deuterophlebiidae possess eversible, crochet-tipped prolegs on abdominal segments I-VII. Nymphomyiidae also have eversible prolegs on the last segment (probably segment IX), though the structure of these prolegs is

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[1] The mandibular comb (*sensu* this analysis) is not homologous to the mandibular comb (*sensu* Wood and Borkent 1989) of Ptychopteromorpha + Culicomorpha; the latter was described as a "comb-like or brush-like row of long, curved setae along dorsal surface". The mandibular comb of the Blephariceromorpha consists of modified apical teeth, rather than modified macrotrichia (see also Courtney *in press*).

slightly different from those on preceding segments (*personal observation*; Cutten and Kevan 1970) and it is unclear if they are serially homologous[1]. Among Blephariceridae, instar I larvae of the subfamily Blepharicerinae possess eversible, crochet-tipped, lateral prolegs on the cephalothorax and each of abdominal segments II-VI. Zwick (1977) considered eversible prolegs a synapotypy of Blepharicerinae, implying the feature was not part of the Blephariceridae groundplan. As discussed elswhere (Courtney *in press 1*), and in agreement with Wood and Borkent (*in press*), I believe presence of eversible, crochet-tipped prolegs is a synapotypy at a higher level, supporting monophyly of the Blephariceromorpha. Lack of eversible prolegs in the blepharicerid subfamily Edwardsininae is considered secondarily derived. Therefore, I assume the following transformation sequence: (**0**) abdominal segments I-VII without lateral prolegs; (**1**) abdominal segments I-VII each with a pair of elongate, eversible, crochet-tipped, lateral prolegs; (**2**) lateral proleg vestigial on abdominal segment VII, and all prolegs lacking eversible crochets in instars II-IV; (**3**) eversible, crochet-tipped, lateral abdominal prolegs vestigial in instar I.

Character 12. *respiration via at least one spiracular opening (plesiotypic) / respiration exclusively cuticular, with spiracular openings vestigial (*i.e.*, apneustic) (apotypic).*

According to Teskey (1981), the groundplan number of spiracles for Diptera larvae is ten pairs (*i.e.*, holopneustic), though this state occurs only in certain Bibionomorpha. In most groups, the number has been variously reduced, with the amphipneustic condition (presence of only an anterior and posterior pair of spiracles) the most common. The complete loss of spiracles, or apneustic condition (or, in the present context, the apotypic state) occurs only in aquatic groups, including all members of the Blephariceromorpha, Simuliidae, and Ceratopogonidae, most Chironomidae, and some Chaoboridae (Teskey

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[1] The presence of these "anal prolegs" may be another apotypy of the family, or perhaps even indicate affinities with other clades (*e.g.*, Culicomorpha).

1981), Tipulidae and Mycetophilidae (Hennig 1973). Although this condition has arisen independently in several groups, it is considered a synapotypy of the Blephariceromorpha.

Character 13. *anal papillae retractable (plesiotypic) / anal papillae permanently exserted, nonretractable (apotypic).*

Anal papillae are characteristic of almost all aquatic and semi-aquatic Nematocera, and are thought to have an osmoregulatory and, in some taxa, respiratory function (Komnick and Wichard 1975). Anal papillae, which also occur in certain Mecoptera (*i.e.*, Nannochoristidae), may have evolved independently in several nematocerous groups (all of which are aquatic): (1) Tipulomorpha; (2) Axymiomorpha; (3) Blephariceromorpha; (4) Psychodidae; and (5) Ptychopteromorpha + Culicomorpha. Alternatively, anal papillae may be a groundplan feature of the latter three groups combined, or perhaps even of all Nematocera. Papillae are lacking from predominantly terrestrial groups, including all Bibionomorpha, most Psychodomorpha, and some Tipulomorpha.

According to Wood and Borkent (*in press*), anal papillae are retractable in the Nannochoristidae (Pilgrim 1972), Ptychopteridae[1], Dixidae, Simuliidae, and Ceratopogonidae (Wirth and Grogan 1979). The plesiotypic state is also typical of the Tipulidae (Brindle 1957), Thaumaleidae (Thienemann 1909), and perhaps Perissommatidae (Colless 1962). Wood and Borkent (*loc. cit.*) used the apotypic state (their character 73) to help define the Corethrellidae + Chaoboridae + Culicidae. Permanently exerted anal papillae are also characteristic of all Blephariceromorpha (*e.g.*, Figs. 4.11, 4.12, A.16), Tanyderidae[2] and apparently of Axymiomorpha (Wood 1981). The apotypic state probably has evolved independently in each of these groups, and in the Culicoidea. See also characters 53 and 54.

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[1] The anal papillae of Ptychopteridae may not of themselves be retractable; their "retraction" may simply reflect the action of the long, retractile respiratory siphon, rather than any action imparted by the papillae.

[2] Wood and Borkent (*loc. cit.*) reported that the anal papillae of Tanyderidae are retractable, a conclusion apparently based on Exner and Craig (1976). Exner and Craig did not mention retractable anal papillae, though retractable "tracheal gills" and "pseudopods" were noted; in fact, the anal papillae of Tanyderidae (*i.e.*, *Protanyderus*) seem to be permanently exerted (*personal observation*; Craig 1989, *personal communication*).

3.5.5.2 Adult

Character 14. *empodium pulvilliform (plesiotypic) / empodium setiform (apotypic).*

In most Nematocera, the acropod bears a pulvilliform empodium[1]. Setiform empodia are reported for only the Nymphomyiidae (Tokunaga 1935; see Fig. A.23), Deuterophlebiidae (female adults; see Fig. 4.66), and Culicomorpha (McAlpine 1981). Blephariceridae and Tanyderidae apparently lack an empodium. This analysis assumes the following transformation sequence: (**0**) empodium pulvilliform; (**1**) empodium setiform; (**2**) empodium vestigial. I assume that the Blepharicеromorph groundplan included a setiform empodium, but consider the evidence supporting this synapotypy rather weak.

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[1] In agreement with Wood and Borkent (*in press*), I see no difference between the arolium of Tipulidae and empodium of other Diptera; therefore, I treat these structures as homologues.

3.5.6 Superfamily Nymphomyioidea - Groundplan Apotypies

3.5.6.1 Larva

Character 15. *tentorium consists of two pairs of tentorial pits and well-developed anterior and posterior tentorial arms (plesiotypic) / tentorium vestigial, with tentorial arms and posterior tentorial pit not apparent (apotypic).*

Primitively, the tentorium of larval Diptera consists of anterior and posterior pits, and well-developed anterior and posterior arms, the latter of which are extended medially and united to form a posterior bridge (Anthon 1943; Hennig 1973). The posterior arms are reduced in most Nematocera (see Courtney *in press 1*). Larval Blephariceridae (Anthon and Lyneborg 1968) and Deuterophlebiidae possess well-developed anterior and posterior arms, but lack a posterior bridge. As discussed earlier, the tentorium of larval Nymphomyiidae is greatly reduced, with tentorial arms and posterior pits not apparent (*personal observation*). A similar, but presumably non-homologous, condition occurs in most Psychodidae (Anthon 1943), Chironomoidea (*sensu* Teskey 1981, but see Gouin 1959), Tipulidae (Cook 1949) and Sciaroidea (*sensu* Teskey 1981).

Reduction or loss of the tentorium may be correlated with hypostomal development and ventral fusion of the cranium (Courtney *in press 1*; Anthon 1943; Hennig 1973; Teskey 1981). If so, these character states may represent a "functional complex". However, because tentorial reduction apparently has occurred independently in many Diptera, it does not provide strong evidence of phylogenetic relationships. In fact, some clades (*e.g.*, Psychodomorpha, Bibionomorpha) demonstrate almost all stages of tentorial development (*i.e.*, from the presumed groundplan condition to a tentorium that is rudimentary), supporting further the contention that tentorial characteristics are homoplastic.

Character 16. *postmental sclerite (=hypostoma) simple and separated from the postgenal margin by essentially membranous cuticle (plesiotypic) / postmental sclerite (=hypostoma) anteriorly serrate and solidly fused to a postgenal bridge (apotypic).*

As discussed at length elsewhere (Courtney *in press 1*), homologies of the ventral cranium are controversial, and development of a postgenal bridge and/or anteriorly serrate postmentum (hypostoma) may be homoplastic. The presumed plesiotypic state for Diptera occurs in relatively few taxa (*e.g.*, Anisopodidae (Anthon 1943); Blephariceridae (Anthon and Lyneborg (1968)), while the apotypic condition apparently has arisen in several clades, including the Nymphomyiidae, Tipulidae, and Chironomoidea. The apotypic state, as defined above, probably reflects a transformation series, with the following steps involved (not necessarily in given order): (1) inward migration of the prementum and concomitant anterior migration of the postmentum; (2) formation of a row of teeth on the anterior margin of the postmentum; (3) fusion of the postgenae, to form a postgenal bridge; and (4) fusion of the posterior and lateral margins of the postmentum with the postgenal bridge.

Character 17. *prolegs on abdominal segments I-VII with monomorphic crochet (plesiotypic) / prolegs on abdominal segments I-VII with dimorphic crochets (*i.e.*, simple and pectinate) (apotypic).*

Proleg crochets of instar I Blepharicerinae are in the form a single row of simple, recurved hooks at the apex of each proleg (Fig. A.5, A.6), and crochets have the same structure on all prolegs. In Deuterophlebiidae, crochets differ between instar I and later instars. The proleg of an instar I larva has a single row of multi-toothed crochets, with each crochet oriented perpendicular to proleg surface (Fig. 2.37). Proleg crochets of later instars (II, III, and IV) are apically recurved, with five uniformly sized tines oriented parallel to proleg surface (Fig. 2.39, see character 52). However, crochet dimorphism does not exist on the same proleg, nor on the same individual or instar. In contrast, the abdominal prolegs (segments I-VII) of late-instar nymphomyiid larvae bear both simple and pectinate crochets (Fig. A.17; Cutten and Kevan 1970; Rohdendorf and Kalugina 1974).

Character 18. *Malpighian tubules four or five in number, with tubule arrangement various (plesiotypic) / Malpighian tubules two in number, with both tubules borne on a common stalk originating on the ventral surface of the gut (apotypic).*[1]

The primitive number of Malpighian tubules for insects is probably six (Wheeler 1893), which corresponds to the number of longitudinal folds in the proctodaeal wall (Snodgrass 1935). Six tubules are characteristic of most Lepidoptera and all Trichoptera (Snodgrass 1935), and probably all Mecoptera; among the latter, six tubules have been reported in Nannochoristidae (Pilgrim 1972), Panorpidae and Boreidae (Potter 1938). However, the Siphonaptera possess only four tubules (Sharif 1937). Because of the difference in tubule number in Mecoptera and Siphonaptera, it is difficult to postulate the groundplan number for Diptera. However, for reasons given below, I assume that the groundplan number for Diptera is four tubules.

The number and arrangement of Malpighian tubules in Diptera are summarized in Table 2. The maximum number of tubules in Diptera is five, which is characteristic of the Deuterophlebiidae, Blephariceridae, Psychodidae, Tanyderidae, Ptychopteridae and Culicidae. Most Diptera possess four tubules, and, as mentioned above, this condition is also characteristic of the presumed immediate outgroup (Siphonaptera). This supports the hypothesis that that four tubules is the groundplan state for Diptera. If this interpretation is accepted, the presence of five tubules in most of Hennig's (1973) Psychodomorpha[2] may represent a synapotypy. Outside of this taxon, only the Culicidae possess five tubules. However, if the classification of Wood and Borkent (*in press*) is accepted, the presence of five tubules in several presumedly unrelated families must be interpreted as either symplesiotypic or, alternatively, the result of convergence. The latter suggests that the five-tubuled condition arose independently in four clades: (1) Blephariceroidea; (2) Psychodidae; (3) Ptychopteromorpha; and (4) Culicidae. Alternatively, the presence of five tubules may be plesiotypic; however, this would require independent reduction in tubule-number in Tipulomorpha, Nymphomyiidae, Psychodomorpha (exclusive of Psychodidae), Axymiomorpha, Bibionomorpha, and several lineages of the Culicomorpha (*i.e.*, Dixidae, Corethrellidae, Chaoboridae, and Chironomoidea). If the Wood and Borkent phylogeny is accepted, the former hypothesis is far more parsimonious.

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[1] In most Diptera, the number and arrangement of Malpighian tubules remains constant between the larva and adult (*personal observation*); therefore, it is assumed that this character also applies to the adult.

[2] This taxon included the Deuterophlebiidae, Blephariceridae, Tanyderidae, Ptychopteridae, Psychodidae, and Nymphomyiidae. All but the Nymphomyiidae possess five Malpighian tubules.

Regardless of the groundplan state for Diptera, the number and arrangement of Malpighian tubules in Nymphomyiidae is derived. Adults of *Nymphomyia alba* Tokunaga (Tokunaga 1936) and larvae and adults of *Palaeodipteron walkeri* (*personal observation*) each possess two Malpighian tubules, with both tubules borne on common stalk originating on the ventral surface of the gut. This condition presumably is characteristic of the family, and is considered a synapotypy of the Nymphomyiidae. Two non-stalked tubules are typical of some Ceratopogonidae (Lawson 1951) and Cecidomyiidae (Krivosheina 1969), suggesting that reduction in tubule number may be susceptible to homoplasy, and possibly allometric. See also characters 39, 54 and 62.

Character 19. *ventral surface of labrum-epipharynx set with simple macrotrichia (plesiotypic) / ventral surface of labrum-epipharynx bearing several rows of pectinate or spatulate macrotrichia (apotypic).*

The plesiotypic condition is typical of most Nematocera, including first instar Deuterophlebiidae. The epipharyngeal surface of a late-instar deuterophlebiid larva bears several rows of modified macrotrichia, the apices of which are expanded, laterally curved, and dissected into several tines (Fig. 2.25). In deuterophlebiids, spatulate macrotrichia apparently are formed by the fusion of several simple macrotrichia (Courtney *in press 1*).

Pectinate macrotrichia are on the epipharynx of larvae of Nymphomyiidae (*i.e.*, in late-instar *Nymphomyia* (Rohdendorf and Kalugina 1974) and *Palaeodipteron* (Fig. A.14; Cutten and Kevan 1970)) and some Chironomidae (*e.g.*, *Chironomus* Meigen, *Micropsectra* Kieffer (Oliver and Roussel 1983)). With regard to the epipharyngeal macrotrichia of these taxa, I am unaware of the condition in first instars, or the mechanism by which these macrotrichia are formed. However, I assume that spatulate or pectinate macrotrichia have evolved independently in each of the Deuterophlebiidae, Nymphomyiidae, and Chironomidae.

3.5.6.2 Pupa

Character 20. *head hypognathous (plesiotypic) / head prognathous (apotypic)* — (Wood and Borkent *in press*).

As pointed out by Wood and Borkent (*loc. cit.*), a hypognathous pupal head is characteristic of Diptera, Siphonaptera, and Mecoptera. The prognathous pupal head (Fig. A.18), apparently typical of all nymphomyiid pupae (Tokunaga 1936; Ide 1965; Cutten and Kevan 1970; Rohdendorf and Kalugina 1974), is clearly an autapotypy.

3.5.6.3 Adult

Character 21. *compound eyes widely separated ventrally (plesiotypic) / compound eyes ventrally contiguous or holoptic (apotypic).*

Except for the Tipulomorpha, all infraorders contain representatives in which the compound eyes are dorsally holoptic (*i.e.*, eye facets contiguous along midline). In most groups, holoptic eyes occur only in males, and this condition is probably associated with aerial swarming and mating (McAlpine and Munroe 1968). Among the Blephariceromorpha, the eyes of only certain male Blepharicerinae are dorsally holoptic.

Although dorsally holoptic eyes are common in many Nematocera, few groups (*e.g.*, Dixidae (Peters 1981)) have eyes that are more widely separated dorsally than ventrally. Only in the Nymphomyiidae are the eyes ventrally contiguous (Fig. A.20), and this feature is considered an autapotypy of the family.

Character 22. *tentorium consists of anterior and posterior tentorial pits, and well-developed tentorial arms (plesiotypic) / tentorium vestigial (apotypic).*

The tentorium of adult Diptera is usually well-developed, consisting of paired anterior, dorsal, and posterior arms, and anterior and posterior tentorial pits (Hennig 1973; McAlpine 1981). All but the dorsal tentorial arms are well-developed in Blephariceridae and Deuterophlebiidae. The tentorium of adult Nymphomyiidae apparently is vestigial, lacking even the remnants of tentorial pits (Tokunaga 1935). Although this condition and character 25 (see below) are considered separate apotypies, it is possible that both are related. The larval tentorium is also vestigial (see character 15), and a similar arrangement in the adult (as well as other features; see character 26) may suggest neotenic retention of larval characters (Tokunaga 1935).

Character 23. *antenna elongate and multi-articled, with flagellum typically of seven or more flagellomeres (plesiotypic) / antenna short, with clavate flagellum of three apparent flagellomeres (apotypic).*

The number of flagellomeres in the Nematocera groundplan is thought to be 14 (Hennig 1973). However, both increases and decreases in the number of flagellar articles have occurred in several groups, with the overall range from a minimum of a single flagellomere in the chironomid *Oreadomyia* (Oliver 1981), to a maximum of 111 flagellomeres in an Afrotropical species of Psychodidae (Quate and Vockeroth 1981). In terms of the general shape and reduction in the number of flagellomeres, the antenna of *Oreadomyia* closely resembles that of a nymphomyiid; in fact, this resemblance was the primary criterion for the original placement of *Oreadomyia* in the Nymphomyiidae (Kevan and Cutten-Ali-Khan 1975). Oliver (1981), based mostly on female genitalic structure, reassigned *Oreadomyia* to the Chironomidae, and suggested that the similarities between *Oreadomyia* and the Nymphomyiidae reflect convergent reduction of flight activity.

While it is generally agreed that the nymphomyiid antenna has only three flagellomeres, some authors have suggested that more segments may be present. In both the North American genus *Palaeodipteron* (Figs. A.19, A.22) and Indian genus *Felicitomyia* Kevan (Cutten and Kevan 1970), the first flagellomere bears distinct annulations, and these annulations may represent actual segments. Ide (1965), in the original description of *Palaeodipteron*, even stated that the adult flagellum consists of "about 30 consolidated segments proximally" (pg. 497). Figures given by Rohdendorf and Kalugina (1974) suggest that antennal annulations are present in *Nymphomyia levanidovae*; however, a comparable arrangement was not reported for *N. alba* (Tokunaga 1935). It remains unclear if flagellar annulations represent true articles, or simply superficial constrictions; however, the generally accepted number of flagellomeres is three (Tokunaga 1935; Cutten and Kevan 1970; Kevan and Cutten-Ali-Khan 1975; Kevan and Cutten 1981). Until further studies indicate otherwise, I accept this interpretation.

Within other members of the Blephariceromorpha, the number of flagellomeres ranges from four in the Deuterophlebiidae to 7-13 in Blephariceridae. I consider the reduced number of flagellomeres in the Nymphomyiidae and Deuterophlebiidae to be the result of convergence. See also character 57.

Character 24. *wing broad, with marginal fringe of relatively short macrotrichia and well-developed anal lobe (plesiotypic) / wing markedly narrow, with marginal fringe of elongate macrotrichia and slightly developed anal lobe (apotypic).*

The plesiotypic condition is characteristic of most Nematocera, including both the Deuterophlebiidae and Blephariceridae. The structure of the nymphomyiid wing is more reminiscent of that of a thysanopteran, rather than a dipteran. Among the Diptera, the cecidomyiid *Ipomyia* Colless (Colless 1965) and some Psychodidae (*e.g.*, *Maruina*) possess similarly narrowed wings, fringed with elongate macrotrichia.

Character 25. *wing with posterior veins distinct and without marked concentration of anterior veins along costal margin (plesiotypic) / wing with posterior veins reduced and anterior veins concentrated along costal margin (apotypic).*

Among the Blephariceromorpha, only the Nymphomyiidae (Tokunaga 1935) exhibit the apotypic state. Although deuterophlebiid wing veins are mostly vestigial, those that are recognizable (see Kennedy 1981) show little evidence of costalization (*i.e.*, posterior veins are no less developed than anterior veins, and anterior veins are not markedly concentrated along the costal margin). In these respects, the deuterophlebiid and blepharicerid wing is similar, with both different from those of nymphomyiid adults. Outside of the Blephariceromorpha, the wings of several taxa (*e.g.*, most Chironomoidea, some Bibionomorpha) show reduction of posterior veins and concentration of anterior veins along the costal margin, the latter of which results in veins of the radial sector terminating in the costa before the wing apex. These similarities are probably convergent.

Character 26. *imago exhibiting "typical" adult characteristics (plesiotypic) / imago neotenic, retaining several larval characteristics (apotypic).*

Several features of the nymphomyiid imago are unusual for adult Diptera, but typical of the larval stage, perhaps indicating neotenic retention of larval characters. Wood and Borkent (*in press*) provide a lengthy discussion of the presence of eight abdominal ganglia in adult nymphomyiids. Although eight ganglia is typical of many nematocerous larvae, the adult nerve cord of all Diptera except Nymphomyiidae is characterized by fusion of at least the last two ganglia. Wood and Borkent point out that fusion of ganglia can be sexually dimorphic (*e.g.*, in some Mecoptera, Siphonaptera), and that Tokunaga's (1936) description of the adult nervous system was based solely on nymphomyiid males. It is unknown if female imagos exhibit a similar arrangement. Wood and Borkent conclude that the presence of eight abdominal ganglia in adult Nymphomyiidae is not plesiotypic, but rather a derived feature, suggesting "neotenic retention of the larval condition".

Several other features may also support an hypothesis of "phylogenetic neoteny" (*sensu* Eldredge and Cracraft 1980). Tokunaga (1935) discussed the resemblance between the nymphomyiid adult cranium and that of larval Nematocera (particularly Chironomidae), including the large occipital foramen and lack of occipital condyles; the presence of a vestigial tentorium (see character 22) may also support a neoteny hypothesis. Tokunaga thought the "lateral organs" or "ocelli" of the adult (Figs. A.19, A.21) were of different origin than the "primary" ocelli of most adult flies (*e.g.*, Blephariceridae). Furthermore, he stated that the ocelli of nymphomyiid adults show "some affinity to the ocelli ... of the larvae of many eucephalous Nematocera" (pg. 158); similar structures (*i.e.*, stemmatic bulla), known to be remnants of the larval eye, occur in adults of certain Simuliidae (Wood 1978; Wood and Borkent 1982) and Chironomidae (Tokunaga *loc. cit.*; Oliver 1981). The presence of "intersegmental sensillae" at the base of the distal flagellomere (Tokunaga *loc. cit.*), which are common on larval, but not adult, antennae, may also indicate neoteny.

Thus, at least five characters (eight abdominal ganglia; large occipital foramen; lack of occipital condyles; "lateral" ocelli; intersegmental antennal sensillae) and possibly others (*e.g.*, vestigial tentorium - see character 22) suggest that nymphomyiid adults have retained larval features. I consider these neotenic "tendencies" as apotypic for Nymphomyiidae.

Character 27. *anterolateral angle of abdominal tergite VIII simple, without prominent tubercle (plesiotypic) / anterolateral angle of abdominal tergite VIII with prominent tubercle or knob (apotypic).*

The plesiotypic state is typical of most Nematocera, including the Blephariceroidea. The apotypic condition apparently occurs only in Nymphomyiidae. Other structures found in males of the genus *Nymphomyia*[1] include the so-called "paratergal projections", which consist of one (Rohdendorf and Kalugina 1974) or two (Tokunaga 1935) pairs of elongate, posteriorly extended appendages on the posterior margin of tergite VIII.

Character 28. *"primary" ocelli present (plesiotypic) / "primary" ocelli absent (apotypic).*

Wood and Borkent (*in press*) use the absence of ocelli as an apotypy of the Culicomorpha + Ptychopteromorpha, even though they acknowledge that it may be a rather homoplastic feature. Ocelli are also lacking in the Tipulomorpha, Nymphomyiidae, Deuterophlebiidae, Psychodidae, and some Cecidomyiidae. In agreement with Tokunaga (1935) and as discussed above (character 26), I do not consider the "lateral" ocelli of Nymphomyiidae as homologous to the "primary" ocelli of most Diptera (*e.g.*, Blephariceridae). If these structures are in fact homologous, it raises doubt as to the validity of Wood and Borkent's use of the character, since some Culicomorpha have structures (*i.e.*, stemmatic bulla) that may be similar to the lateral ocelli of Nymphomyiidae. I consider loss of primary ocelli a weak synapotypy of the Nymphomyiidae; furthermore, I assume convergent loss of ocelli in adult Deuterophlebiidae.

Character 29. *mouthparts and digestive tract well-developed (plesiotypic) / mouthparts and digestive tract predominantly atrophied (apotypic).*

In a generalized dipteran, adult mouthparts are in the form of a proboscis composed of several recognizable elements, including a well-developed labrum, labium, hypopharynx, and paired mandibles and maxillae (Teskey 1981). Certain of these structures, especially mandibles, are lost in various nectarivorous or non-feeding taxa (*e.g.*, some Blephariceridae). The mouthparts of an adult Nymphomyiidae (Fig. A.20) consist of a small circular oral opening, surrounded by a dorsal, beak-like lobe (labrum?) and a pair of ventral lobes, each bearing a cluster of setiform sensilla (labium?); within the oral opening is a small, branched structure (possibly the hypopharynx). None of these mouthparts appear to be articulated or in any way movable, and it appears that these flies are unable to feed. However, several muscles insert on the pharynx and oesophagus, and the salivary glands are apparently well-developed (Tokunaga 1935), both of which suggest that adults are at least capable of imbibing fluids. Although the digestive system of a nymphomyiid imago is more or less complete (*i.e.*, in terms of recognizable elements), its constituent elements are in fact rather reduced; furthermore, histological research has demonstrated a lack of digestive function (Tokunaga 1936). These data suggest that adult Nymphomyiidae are non-feeding and short-lived. Mouthpart and digestive tract reduction, aphagia, and/or a brief life are also characteristic of the imagos of other Diptera (*e.g.*, Deuterophlebiidae (see chapter 5), certain Chironomidae (Tokunaga 1932a; Neumann 1976)). These similarities are presumed to be convergent.

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[1] Kevan and Cutten (1981) report that, in addition to anterolateral tubercles, tergite VIII of *Palaeodipteron* bears "long bifid backwardly directed paratergal projection[s]" (pg 210); however, I am unable to see anything resembling paratergal projections in either their figures, or in actual specimens of *Palaeodipteron*. Paratergal projections would, therefore, seem to be unique to the genus *Nymphomyia*.

Character 30. *wings remain attached throughout adult life (plesiotypic) / wings deciduous, shed after flight and/or during oviposition activities (apotypic).*

In some Nymphomyiidae (*e.g.*, *Palaeodipteron*), the male and female shed their wings after emergence, presumably during oviposition activities (Ide 1964, 1965; Cutten and Kevan 1970; Back and Wood (1979)). This condition may apply to all members of the family; however, definitive evidence of deciduous wings is lacking for the genera *Nymphomyia* and *Felicitomyia*. Post-emergence loss of wings also is characteristic of female Deuterophlebiidae (*personal observation*; Wood and Borkent *in press*), and is related to oviposition behaviour (see chapter 5). In agreement with Wood and Borkent (*loc. cit.*), I assume that deciduous wings have evolved independently in Nymphomyiidae and Deuterophlebiidae.

Character 31. *femur and tibia uniformly sclerotized, undivided (plesiotypic) / femur and tibia each subdivided by apparently membranous cuticle into short, basal zone and elongate, distal zone (apotypic).*

Both the femur and tibia of adult Nymphomyiidae are subdivided by apparently membranous cuticle (Tokunaga 1935), a condition that Wood and Borkent (*in press*) considered autapotypic for the family. Although Nymphomyiidae are the only Diptera that possess a subdivided tibia, the presence of a subdivided femur is also typical of adult Deuterophlebiidae (Courtney *in press 2*)[1]. Again, this similarity between Nymphomyiidae and Deuterophlebiidae is considered the result of convergence, perhaps due to constraints of the pupal case and the brief imaginal life (Courtney *loc.cit.*).

Character 32. *spiracles present on abdominal pleurites (plesiotypic) / abdominal spiracles absent (apotypic).*

In adult Diptera, the primitive number of abdominal spiracles is eight (Crampton 1942), and the presence of seven or eight is typical of most groups (McAlpine 1981). All abdominal spiracles are vestigial, presumably by convergence, in only a few groups, including Nymphomyiidae, Deuterophlebiidae, and certain Psychodidae (Tokunaga 1935).

Character 33. *spermathecae present, usually three in number (plesiotypic) / spermathecae absent (apotypic).*

The presence of three spermathecae is considered plesiotypic for Diptera (Downes 1968; Hennig 1973), and this number is characteristic of at least some members of all infraorders. Although some Blephariceridae (*e.g., Paulianina*) possess only two spermathecae, three is typical of most taxa (Hogue 1981), and probably represents the groundplan condition for the Blephariceromorpha. The Deuterophlebiidae, and perhaps also Nymphomyiidae[1], lack spermathecae. This similarity is presumably convergent, and reflects the fact that females are short-lived and require no elaborate sperm-storage organs. Although considered apotypic for each of the Nymphomyiidae and Deuterophlebiidae, absence of spermathecae is not unique to these taxa. Spermathecae are apparently vestigial or absent from the Thaumaleidae and some Cecidomyiidae[2] (Saether 1977).

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[1] Tokunaga (1935, pg. 184, footnote 17) reached a similar conclusion.

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[1] No published descriptions (*e.g.*, Tokunaga 1935; Ide 1965; Cutten and Kevan 1970) mention whether or not nymphomyiid females possess spermathecae. This and nymphomyiid mating behaviour (*i.e.*, at least in *Palaeodipteron* (see Ide 1965; Cutten and Kevan 1970)) suggest that sperm storage is not necessary. Therefore, I assume that spermathecae are absent. Spermathecae were not apparent in material examined personally; however, material was somewhat damaged and possibly unsuitable for evaluating the character.

[2] According to Saether (1977), vestigial spermathecal ducts (two) are still evident.

3.5.7 Superfamily Blephariceroidea - Groundplan Apotypies

3.5.7.1 Larva

Character 34. *instar I frontal sclerite and clypeus contiguous (≈ frontoclypeal apotome), not separated by band of membranous cuticle (plesiotypic) / instar I frontal sclerite isolated, separated from clypeus by a band of membranous cuticle (apotypic)* (*).

The plesiotypic state is characteristic of all Diptera for which first instar larvae are known. An isolated frontal sclerite bordered by membranous cuticle apparently occurs only in larval instar I of Deuterophlebiidae and Blephariceridae (Courtney *in press 1*). A similar, but presumably non-homologous, condition is found in certain Bibionidae (Teskey 1981[1]). Courtney (*loc. cit.*) argued that the frontal sclerite of instar I Deuterophlebiidae and Blephariceridae is not homologous to the frons of other insects, nor does the membranous cuticle at the sclerite's anterior border represent a "frontoclypeal suture" (*sensu* other insects). In larvae of both families, this condition probably reflects desclerotization of the dorsal cranium or, alternately, precocious hatching of larvae (Courtney *loc. cit.*). Regardless, the isolated frontal sclerite of instar I is considered a synapotypy of the Blephariceroidea.

Character 35. *antennal socket occupies an anterodorsal position, in close proximity to the peristomal margin (plesiotypic) / antennal socket occupies a more lateral position, comparatively distant from the peristomal margin (apotypic).*

In most Diptera, the antenna occupies an anterodorsal position, usually close to the peristomal margin. In larvae of the Blephariceroidea, the antennal socket occupies a posterolateral position, well within the genal margin and relatively distant from the frons and peristomal margin. As discussed elsewhere (Courtney *in press 1*)), this positional shift may be advantageous in torrential habitats, to enhance streamlining and keep the elongate antenna in lower current velocities of the boundary layer. The adaptive nature of this character state may suggest independent evolution in both families; for the present, however, I assume this shift in antennal position reflects common ancestry, rather than adaptive convergence.

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[1] Frontoclypeal apotome and "frontoclypeal suture" of late-instar *Bibio* (pgs. 66-67).

Character 36. *postmentum in the form of a broad, well-sclerotized plate (plesiotypic) / postmentum predominantly membranous, particularly in early instars (apotypic).*

Structural modifications of the labium and postgena were discussed at length by Courtney (*in press 1*). In larvae of most nematocerous flies, the postmentum (= hypostoma) is a broad, well-sclerotized plate, often occupying a large portion of the ventral cranial surface. The deuterophlebiid postmentum is relatively expanded, but consists exclusively of membranous cuticle. Desclerotization of the postmentum is also evident in larval Blephariceridae, though a small postmental sclerite is retained in some taxa (Anthon and Lyneborg 1968). Nearctic species of blephariceríds demonstrate a similar condition; however, postmental sclerites are not evident in early-instar (I-III) larvae, and ill-developed in mature (instar IV) larvae of only a few species (*e.g.*, *Agathon comstocki*). Desclerotization of the postmentum, particularly in early instars, is considered a synapotypy of the Blephariceroidea. Data for other nematocerous groups is needed to evaluate this ontogenetic trend in postmental development.

Character 37. *posterodorsal margin of cranium entire, and incapable of intermolt cuticle deposition (plesiotypic) / posterodorsal margin of cranium laterally excised or medially extended into prothorax, and with a region of intermolt cuticle deposition (apotypic).*

The posterodorsal cranial margin is excised laterally in many Blephariceridae (most members of the subfamily Blepharicerinae). In contrast, the cranial margin is entire or only slightly excised in larvae of the subfamily Edwardsininae and some of the more "primitive"

(Zwick 1988, *personal communication*) Blephariceriniae (*e.g.*, *Bibiocephala*, some *Agathon*). In these taxa, all but the last instar larva demonstrate an unusual cranial modification, in the form of a transverse, posteriorly excised, sclerotized strip. This strip extends posteriorly from the cranial margin to beneath the cephalothoracic integument, and has been variously identified as a cranial (Tonnoir 1924) or thoracic (Stuckenberg 1958) element. Data for Nearctic blepharicerids confirms Tonnoir's theory about the origin of this sclerotized strip. Examination of larvae of various ages demonstrates that this sclerotized strip is in fact an extension of the cranial margin deposited during the intermolt period. The increased surface area created by this sclerotized zone accommodates attachment of the large mandibular adductor muscles, which also increase in size during the intermolt period.

Zwick (1977) concluded that the blepharicerid groundplan included a cranium with an entire posterodorsal margin. This condition appears to be correlated with the presence of intermolt cuticular extensions; thus, the latter may also be a plesiotypic feature. Interestingly, blepharicerids with pre-existing cranial excisions (*e.g.*, *Blepharicera* spp.) do not demonstrate intermolt cranial extension (though mandibular muscles evidently do undergo some growth (*personal observation*)).

The posterodorsal margin of the deuterophlebiid cranium is medially extended into the prothorax (Courtney *in press 1*), in a region where cuticle deposition continues during the intermolt period. The extent of this zone is not as great as in the Blephariceridae; nonetheless, its presence is considered a synapotypy of the two families.

A comparable arrangement has been described in certain Tipulidae (Pritchard 1982; Pritchard and Mutch 1984), and may also occur in some Tanyderidae (Anthon 1988). The phylogenetic implications of this pattern are unclear, partly because of the paucity of developmental information on most groups. I assume that the apotypic state has arisen independently in each of the Tipulidae, Blephariceroidea, and Tanyderidae. It is possible that this character and the next (character 38) are related.

Character 38. *head and prothorax distinct, separable by lateral incisions (plesiotypic) / head and prothorax indistinguishably fused in early instars (I and II) (apotypic).*

In larvae of most Nematocera, the head and prothorax are distinct and usually separable by lateral incisions. The head and prothorax of early-instar (I and II) Deuterophlebiidae consist essentially of a single unit, separable only by the position of prothoracic sensilla. In all larval instars, the dorsomedial cranium is intimately united with, and posteriorly extended through, the prothorax. Morphology of early-instar deuterophlebiids suggests a precursor of the blephariceerid cephalothorax, which consists of a fused head, thorax, and abdominal segment I. Fusion of anterior segments (or a tendency toward cephalothorax formation) is considered a synapotypy of the Blephariceroidea, and part of the following transformation sequence: (**0**) head and prothorax distinct and separable by lateral incisions; (**1**) head and prothorax indistinguishably fused, at least in early instars; (**2**) head, thorax, and abdominal segment I fused (= cephalothorax) in all instars. The latter, of course, is one of the most striking characteristics of the Blephariceridae. Although I assume that these character states are part of a transformation, they may in fact be unrelated. In addition to the Deuterophlebiidae, the intermediate state may occur in larval Tipulidae, Tanyderidae, and Axymyiidae. This could suggest that the character is either homoplastic, or has no phylogenetic bearing on the eventual formation of the blephariceerid cephalothorax. For the present, I accept this character as only a weak indicator of the monophyly of Blephariceroidea.

Character 39. *Malpighian tubules four in number (plesiotypic) / Malpighian tubules five in number (apotypic).*

I have argued (character 18) that the groundplan number of Malpighian tubules in Diptera equals four. Therefore, the presence of five tubules is interpreted as a derived, but evidently homoplastic, feature. Accepting the Wood and Borkent (*in press*) phylogeny, the five-tubuled condition has evolved independently in each of the Blephariceroidea, Psychodidae, Ptychopteromorpha, and Culicidae.

3.5.7.2 Pupa

Character 40. *pupa elongate-cylindrical in shape and not attached to the substrate, with tergites and sternites of uniform sclerotization (plesiotypic) / pupa dorsoventrally flattened and immovably attached to the substrate by 3-4 pairs of ovoid, ventrolateral adhesive discs, with tergites darkly sclerotized and sternites essentially membranous (apotypic).*

Pupae of the Blephariceroidea demonstrate several compelling synapotypies. The dorsoventrally flattened, streamlined shape, and abdominal cuticle that is thick and well-sclerotized dorsally but essentially membranous ventrally, are unusual for Diptera pupae. Except for deuterophlebiids and blepharicerids, this condition occurs only in certain Psychodidae (*e.g.*, *Maruina*) and Ephydridae (*e.g.*, *Diedrops* Mathis and Wirth). Like deuterophlebiids and blepharicerids, these taxa inhabit areas of rapidly flowing water and, thus, belong to a "guild" of torrenticolous specialists (Mathis and Hogue 1986). Adaptive convergence due to habitat may account for some similarities in pupal shape and structure between *Maruina*, *Diedrops*, and the Blephariceroidea. However, I believe similarities within the latter group also reflect common ancestry. This view is due, in part, to the shared presence of ventrolateral adhesive discs on the pupal abdomen. Adhesive discs are situated on abdominal segments III-V in the Deuterophlebiidae and segments IV-VI in most Blephariceridae (segments III-VI in the tribe Apistomyiini), and are apparently unique to these families[1]. A detailed study of the formation and microstructure of adhesive discs may be necessary to establish definitive homologies; unfortunately, such an investigation has never been done. For the present, I treat these features as synapotypic for the Blephariceroidea, a conclusion that was also reached by Wood and Borkent (*in press*).

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[1] Superficially similar structures occur on the ventral surface of abdominal segments V-VII in the Psychodid genus *Sycorax* (Haliday) Walker (Feuerborn 1932).

Character 41. *thoracic respiratory organ absent (plesiotypic) / thoracic respiratory organ in the form of a plastron-bearing spiracular gill that acquires its final volume and shape before the larval-pupal ecdysis (apotypic).*

Plastron-bearing spiracular gills are characteristic of the Deuterophlebiidae (Hinton 1962), Blephariceridae (Hinton 1962), Simuliidae (Hinton 1957), Thaumaleidae (Currie 1989, *personal communication*) and certain Tipulidae (Hinton 1955, 1965, 1966a), Tanyderidae (Hinton 1966b), Chironomidae (Coffman 1979), and brachycerous flies (Hinton 1966c). Except for Deuterophlebiidae and Blephariceridae, multi-branched gills occur only in the Simuliidae and certain Tipulidae and Chironomidae. Hinton (1966b) proposed independent evolution of plastron-bearing spiracular gills in at least six nematocerous groups; however, it seems more likely that these structures have arisen no more than four times in these flies: (1) limoniine Tipulidae; (2) Blephariceroidea; (3) Tanyderidae (*Eutanyderus* Alexander); and (4) Chironomoidea (Currie 1989, *personal communication*). In only the Blephariceroidea are the gills pre-hardened and fully formed (*i.e.*, with their final volume and shape) *before* the larval-pupal ecdysis (Hinton 1962).. I assume the following transformation sequence: (**0**) thoracic respiratory organ absent or, if present, lacking a plastron network; (**1**) thoracic respiratory organ in the form of a plastron-bearing spiracular gill; (**2**) thoracic respiratory organ in the form of a plastron-bearing spiracular gill that acquires its final volume and shape before the larval-pupal ecdysis. I treat this combination of features as a synapotypy of the Blephariceroidea.

Isolated blood and epidermis have been found in almost all taxa with plastron-bearing spiracular gills. As summarized by Hinton (1966a), the fate and function of these isolated tissues varies between groups. Tissues become cuticularized and non-functional in the Blephariceridae, while in the Simuliidae, isolated tissues apparently control the size of the gill (*i.e.*, until the basal fenestra ruptures). Isolated tissues are evidently responsible for gill expansion and damage repair in certain limoniine Tipulidae (*e.g.*, *Taphrophila*, *Orimargula*). In other limoniines (*e.g.*, *Lipsothrix*), and in Deuterophlebiidae, these cells remain in "good condition" (Hinton 1962) and may contribute to gill repair. However, Hinton (1962) suggested that the presence of isolated tissues in deuterophlebiid gills may simply be a mechanical artifact of the moulting process and of no substantive function.

Character 42. *adult wing developing within pupal wing sheath as an unexpanded version of its final form, with expansion only after emergence (plesiotypic) / wing reaching its final size and shape before emergence, and unfolding and immediately functional at emergence (apotypic).*

With regard to this character, I concur with the interpretations of Hennig (1973) and Wood and Borkent (*in press*). The nymphomyiid wing presumably also reaches its final size and shape *before* emergence and is immediately functional at emergence; thus, the apotypic state may support monophyly of the Blephariceromorpha. However, with respect to the pattern of longitudinal wing folds and resultant false veins, the Nymphomyiidae are rather different than either the Deuterophlebiidae or Blephariceridae. Therefore, I assume that the Blephariceroidea and nymphomyiid conditions are not homologous.

3.5.7.3 Adult

Character 43. *meron in the form of a small, triangular sclerite (plesiotypic) / meron large and rounded, as fully developed behind the midcoxa as is the katepisternum in front of the midcoxa (apotypic)* — (Wood and Borkent *in press*).

As discussed by Wood and Borkent (*loc. cit.*), this may be a synapotypy of the Blephariceroidea, even though a comparable arrangement occurs in other groups (*i.e.*, Perissommatidae, Axymiomorpha, and some Tipulomorpha).

Character 44. *wings, at rest, usually held backward and folded over the abdomen (plesiotypic) / wings, at rest, permanently extended above or lateral to body, not held backward and folded over the abdomen (apotypic).*

The plesiotypic state is typical of not only the Diptera, but of most neopterous insects. Variations of this behaviour are evident in some taxa; *e.g.*, many Psychodidae hold their wings in a roof-like position, and certain Tipulidae, Simuliidae, etc. demonstrate several different resting positions (*personal observation*). However, almost all flies seem to be at least *capable* of folding the wings backward over the abdomen. The Deuterophlebiidae and Blephariceridae apparently are exceptions to this pattern.

Adult Deuterophlebiidae maintain the wings in a permanently extended position, and seem incapable of folding the wings backward over the abdomen. As discussed elsewhere (chapter 5), males spend their entire life in flight, can not walk, and apparently do not rest; therefore, it is not surprising that the wings are permanently extended above (*i.e.*, as in Kennedy 1981, Fig. 9.1), or lateral to, the body. In contrast, females are longer-lived, can walk, and occasionally do "rest". Observations of resting females indicate that the wings do not folded over the abdomen, but rather are held upright, flat, or at an intermediate angle to the body.

Contrary to the adult depicted in Hogue (1981, Fig. 8.1), a resting blephariceird does not hold the wings backward over the abdomen (*personal observation*; Hogue 1989, *personal communication*). In fact, the resting position of an adult, with the wings "held flat and at a moderate angle from the body" (Hogue 1981, pg. 194), is rather characteristic of blepharicerids. Comparable descriptions and more accurate illustrations of resting adults are provided by Mannheims (1935, Fig. 17) and Zwick (1977, Fig. 1). This behavioural (and morphological?) character is considered homologous to that in the Deuterophlebiidae, and further evidence of monophyly of the Blephariceroidea.

Character 45. *costal vein extended around margin of wing (plesiotypic) / costal vein absent beyond apex of wing (apotypic).*

The apotypic state is not unique to the Blephariceroidea, but also occurs in some Psychodomorpha, all Chironomoidea and Axymiomorpha, and most Bibionomorpha. I consider this a synapotypy of the Blephariceroidea because the plesiotypic condition is typical of the blephariceroid outgroup (*i.e.*, Nymphomyiidae) and primitive members of the Psychodomorpha (*sensu* Wood and Borkent *in press*). Tipulidae, Ptychopteromorpha, and Culicoidea also demonstrate the plesiotypic state.

Character 46. *male terminalia carried in various positions, but usually not dorsoflexed (plesiotypic) / male terminalia dorsoflexed (apotypic)* — (Wood and Borkent *in press*).

Dorsoflexion of male terminalia is characteristic of both the Blephariceridae and Deuterophlebiidae, at least in preserved specimens (*personal observation*; Wood and Borkent *loc. cit.*). Wood and Borkent acknowledged that, among Nematocera, this condition may not be unique to the Blephariceroidea[1]. Lack of data on adult behaviour in blephariceroid and other taxa also makes this interpretation rather tenuous. However, until contradictory data suggest otherwise, I concur with Wood and Borkent's proposal that dorsoflexion of the male terminalia is a synapotypy of the Blephariceroidea.

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[1] In fact, because this arrangement is typical of the Mecoptera, it may even be plesiotypic for Diptera.

3.5.8 Family Deuterophlebiidae - Groundplan Apotypies

3.5.8.1 Larva

Character 19. *ventral surface of labrum-epipharynx set with simple macrotrichia (plesiotypic) / ventral surface of labrum-epipharynx bearing several rows of pectinate or spatulate macrotrichia (apotypic).*

The apotypic state is characteristic of the Deuterophlebiidae, Nymphomyiidae, and at least some Chironomidae. As discussed above (*re*. Nymphomyiidae), this condition has probably evolved independently in each of these clades.

Character 47. *cranium with dorsal and lateral sclerites variously subdivided by bands of thin, membranous cuticle* (i.e., *ecdysial lines) (plesiotypic) / cranium with dorsal and lateral sclerites solidly and indistinguishably fused, lacking ecdysial lines (apotypic).*

The dorsal and lateral cranial sclerites of a late-instar (instars II, III, and IV) deuterophlebiid larva are solidly fused, and all traces of ecdysial lines have been lost (see Fig. 2.8). As discussed elsewhere (Courtney *in press 1*), this necessitates unusual ecdysial characteristics. No other Diptera, except perhaps some Tanyderidae (Anthon 1988) and Tipulidae (Cook 1949)[1], demonstrate an arrangement that is even remotely comparable; therefore, this cranial structure is considered an autapotypy of the Deuterophlebiidae.

Character 48. *distal antennal article simple (plesiotypic) / distal antennal article bifurcate (apotypic).*

One of the most unusual features of a deuterophlebiid larva is the bifurcate distal antennal article. As discussed elsewhere (Courtney *in press 1*), the presence of a diversity of sensory structures and the haemocoelic continuity with basal articles demonstrate that the distal article is a true article, and not a pair of modified apical sensilla. Many other Diptera (*e.g.*, some Blephariceridae, Nymphomyiidae, Chironomidae) have antennae with superficially "bifurcate" apical structures, but these are clearly modified sensilla, rather than true articles. A truly bifurcate distal antennal article is evidently unique to the Deuterophlebiidae, and is considered an autapotypy of the family.

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[1] Similar cranial structure is reported for instar III *Mischoderus* (Anthon 1988) and for larvae of the limoniine *Dicranota* (Cook 1949); however, other tanyderids and limoniines exhibit a more typical arrangement, with sclerites separable by ecdysial lines.

Character 49. *labrum operated exclusively by muscles originating on non-labral sclerites (plesiotypic) / labrum partly operated by a fully intrinsic muscle, whose origin and insertion are both situated on labral sclerites (apotypic)* (*).

The intrinsic labral muscle, which is laterally extended across the clypeo-labrum (*i.e.*, between the tormae), may play an important role in the operation of this relatively large mouthpart (Courtney *in press 1*). Lack of detailed information on labral musculature for other Nematocera make definitive statements about the distribution of this character difficult; however, it is likely that the presence of a fully intrinsic labral muscle is autapotypic for the Deuterophlebiidae.

Character 50. *hypopharyngeal suspensorium simple in instar I (plesiotypic) / hypopharyngeal suspensorium anteriorly serrate in instar I (apotypic)* (*).

The hypopharynx of an instar I deuterophlebiid is unusual, mostly because of its serrate anterior margin (see Fig. 2.26). Similar structure is unreported for other Nematocera, though studies of early-instars are few, with most pertaining to members of the Culicomorpha. The Nymphomyiidae possess an anteriorly toothed plate beneath the hypostoma ("lingua of the hypopharynx" *sensu* Cutten and Kevan (1970) (see Fig. A.15)). I proposed elsewhere (Courtney *in press 1*) that the nymphomyiid "lingua" is probably part of the prementum, rather than the hypopharynx. Until a detailed morphological study can establish definitive homologies for mouthparts of larval Nymphomyiidae, I accept this interpretation. In some taxa (*e.g.*, Culicomorpha), the hypopharynx and prementum forms a compound structure ("prementohypopharyngeal complex" *sensu* Teskey 1981). The prementum and hypopharynx of certain Tipulidae (*e.g.*, late-instar *Limonia*, *Antocha*) are also complex, with the latter structure apparently anteriorly serrate (see Fig. A.12). It is unknown if a similar arrangement occurs in instar I larvae. For the present, I consider the anteriorly serrate hypopharynx of instar I Deuterophlebiidae an autapotypy of the family.

Character 51. *pharyngeal apparatus present, functioning as either a filtering or grinding and sifting device (plesiotypic) / pharyngeal apparatus absent (apotypic)* (*).

Terms used for modifications of the pharynx appear to be somewhat ambiguous, and brief mention of terminology must precede any discussion of pharyngeal characters. Wood and Borkent (*in press*) considered the pharyngeal "filter" and "apparatus" as non-homologous structures, splitting them into two different character systems: The first (62: "Pharyngeal filter present (plesiomorphic) / Pharyngeal filter absent, replaced by a muscular pharynx (apomorphic)" was used to help define the Simuliidae + (Chironomidae + Ceratopogonidae), while the second (63: "Pharyngeal apparatus absent to somewhat developed (plesiomorphic) / pharyngeal apparatus markedly developed with two strongly diverging arms and rows of combs (apomorphic)") supported monophyly of the Ceratopogonidae. Borkent *et al.* (1987) clearly demonstrated that the "grinding and sifting" pharyngeal apparatus of larval ceratopogonid was unique, and represented a valid synapotypy of the family. Furthermore, and in contrast to Wood and Borkent (*loc. cit.*), Borkent *et al.* (*loc. cit.*) considered the pharyngeal apparatus a "unique modification of the pharyngeal filter" (pg. 395), thus suggesting that both structures were homologous. This problem of homology remains unresolved, particularly in light of recent discoveries about the chironomid *Archaeochlus* (Borkent 1989, *personal communication*). The pharynx of this primitive chironomid apparently has a "basket-like" structure (Borkent 1989, *personal communication*) that is reinforced by a U-shaped strut (Borkent *et al. loc. cit.*). If the pharyngeal basket is in fact a vestigial pharyngeal filter (*i.e.*, the structures are homologous), it suggests that the pharyngeal filter may have been lost independently in chironomids and simuliids, and not as a groundplan apotypy of the Simuliidae + (Chironomidae + Ceratopogonidae).

Until this problem of homology is resolved, I have elected to avoid the term pharyngeal *filter* and use, instead, the more general term *apparatus*. Further justification for this term comes from the fact that the function of the pharynx sometimes varies within a group; *e.g.*, in Ptychopteridae, some groups (*e.g.*, *Ptychoptera*) use the pharynx as a filter, while others (*e.g.*, *Bittacomorpha*) use it to grind food (Wood and Borkent *loc. cit.*).

A well-developed pharyngeal apparatus occurs in the larvae of almost all aquatic Nematocera, including the Ptychopteridae and many Culicomorpha (Borkent *et al. loc. cit.*; Wood and Borkent *loc. cit.*), Tanyderidae (Anthon 1988), Blephariceridae (Anthon and Lyneborg 1968), and some Tipulidae and Psychodomorpha (Anthon 1943). I assume that the pharyngeal apparatus is a groundplan feature of the Blephariceromorpha, and consider its presence in blepharicerids to be plesiotypic, and absence in deuterophlebiids to be an apotypic loss. At present, the pharyngeal structure of larval Nymphomyiidae is unknown.

Character 52. *proleg crochets simple (plesiotypic) / proleg crochets apically with five uniformly sized teeth oriented parallel to proleg surface (apotypic).*

Although the prolegs of Nymphomyiidae bear multi-toothed crochets (see character 17), their structure is markedly different than that of deuterophlebiids. Proleg morphology demonstrates that the proleg crochets of larval Deuterophlebiidae (*i.e.*, in instars II, III, and IV) are unique among Diptera. The presence of these crochets, which are apically recurved and bear five, uniformly sized teeth oriented parallel to the proleg surface (Fig. 2.39), is considered an autapotypy of the Deuterophlebiidae.

Character 53. *four anal papillae (plesiotypic) / five anal papillae (apotypic).*

Among Diptera, only two families possess an odd number of anal papillae: Simuliidae (with three) and Deuterophlebiidae (with five). The groundplan number for the Culicomorpha is probably four (*i.e.*, two pairs), which leads to the question of the origin of the "odd" papilla in black fly larvae. In the larvae of many flies (*e.g.*, Culicidae), four major tracheal tubes reach the anal papillae, with one tube entering each of the four papillae (Snodgrass 1959). As in culicids, the anal papillae of larval Simuliidae house four tracheal tubes; however, two of these tubes enter the middle papilla, while the lateral papillae each contain a single tube (Headlee 1906; Wagner 1926). This tracheal arrangement suggests that the middle papilla may represent a pair of fused ancestral papillae. Alternatively, the middle papilla may have evolved *de novo* as an unpaired lobe. Within the Blephariceromorpha, both the Nymphomyiidae (Fig. A.16) and Blephariceridae have four anal papillae, which is probably the groundplan condition for the infraorder. Thus, the above "fusion" hypothesis presumably can not account for the "fifth" papilla on a larval deuterophlebiid; *i.e.*, unless a two step process is proposed: (1) evolution of a third pair, followed by (2) fusion of one pair. While this is not impossible, alternate hypotheses seem to provide a less complex mechanism. The first of these alternatives is, as for simuliids, that the "odd" papilla has evolved *de novo* as an unpaired lobe.

A second, rather novel, hypothesis, based partly on character 54 (see below), proposes that the fifth "anal papilla" is actually the vestiges of abdominal segment IX. The topology of this region, with the anus effectively separating the "papillae" into a single dorsomedial lobe and four ventrolateral lobes, may indicate that these structures are of different origin, with the dorsomedial lobe representing segment IX and the ventrolateral lobes homologous to "true" anal papillae. As discussed above, the anal papillae of most aquatic Diptera are paired and situated ventral and/or lateral to the anus; this agrees with the interpretation that deuterophlebiid larvae have four anal papillae (two pair) ventrolateral to the anus, and a single lobe (segment IX) dorsomedial to the anus. The Malpighian tubule arrangement, with all five terminating in only four anal papillae and none in the dorsomedial "papilla" (see character 54), suggests further differences in function and origin.

For the present, I consider the dorsomedial papilla a true anal papilla. The presence of five anal papillae is clearly apotypic, and apparently unique to the Deuterophlebiidae.

Character 54. *Malpighian tubules terminate in body cavity (plesiotypic) / Malpighian tubules terminate in anal papillae (apotypic).*

It is well established that anal papillae and Malpighian tubules can play important roles in osmoregulation (Wigglesworth 1938; Brindle 1952; Komnick and Wichard 1975). In most Diptera and, indeed, most insects, Malpighian tubules terminate freely in the body cavity or sometimes penetrate the walls of the rectum. In a few aquatic groups, perhaps to enhance osmoregulatory capabilities in ion-poor aquatic situations (*e.g.*, alpine streams), the distal ends of the Malpighian tubules terminate in the anal papillae. This arrangement occurs in the following taxa (numbers in parentheses refer to # of tubules / # of anal papillae / # of tubules terminating in anal papillae per anal papillae): (a) Nannochoristidae (Mecoptera) (6/2/1) (Pilgrim 1972); (b) Ptychopteridae (5/2/1) (Komnick and Wichard 1975); (c) Tanyderidae (5/4/1) (*personal observation*); and (d) Deuterophlebiidae (5/5/>1). In all but the Deuterophlebiidae, at least one Malpighian tubule terminates freely in the body cavity, with each anal papilla containing only one tubule. In contrast, deuterophlebiid larvae have the distal ends of all five Malpighian tubules terminating in the ventral four anal papillae (see Figs. 4.11, 4.12). Thus, two tubules terminate in one of the four papillae, while none enter the dorsomedial papilla. This suggests that these structures may be physiologically different, and may support the hypothesis that the dorsomedial lobe is in fact a modified "segment IX", rather than a fifth anal papilla.

Regardless of the origin of the dorsomedial anal papilla, the arrangement of Malpighian tubules in the Deuterophlebiidae is unique, and considered an autapotypy of the family. The somewhat similar arrangement in the Nannochoristidae, Ptychopteridae and Tanyderidae, while perhaps supporting monophyly of the latter two families, is presumedly unrelated to the condition in deuterophlebiids.

Character 55. *genae ventromedially extended and united to form a postgenal bridge (plesiotypic) / genae ventromedially separated, not forming a postgenal bridge (apotypic).*

Morphology of the ventral cranium was discussed at considerable length by Courtney (*in press 1*) and only a brief summary is given here. Outgroup analysis supports the hypothesis that the Blephariceromorpha groundplan included a well-sclerotized ventral cranium, and probably even a postgenal bridge. These features are characteristic of most Nematocera, particularly the Nymphomyiidae. The ventral cranium of both the Deuterophlebiidae and many Blephariceridae (subfamily Blepharicerinae) is predominantly membranous, with no evidence of a sclerotized postgenal bridge. Although this could indicate that a membranous ventral cranium is a synapotypy of the Blephariceroidea, morphology of the subfamily Edwardsininae suggests otherwise. Larvae of this group apparently possess a narrow, sclerotized, postgenal bridge (Anthon and Lyneborg 1968), a feature which Zwick (1977) considered plesiotypic. This suggests that lack of a postgenal bridge in the Blepharicerinae and Deuterophlebiidae is convergent, and due to secondary desclerotization of a previously fused ventral cranium. For the present, I accept this interpretation, but acknowledge that lack of ontogenetic information on the Edwardsininae (and other Nematocera) makes phylogenetic conclusions somewhat tenuous (see Courtney *loc. cit.*).

3.5.8.2 Pupa

Character 56. *pupa lacking pre-hardened cuticle, and without thoracic bands and ventrolateral abdominal spines (plesiotypic) / pupa with pre-hardened cuticle in the form of thick, transverse, thoracic bands and ventrolateral abdominal spines on segments I, II, VI and VII (apotypic).*

Several macrosculptural features of the pharate pupa are visible through the cuticle of mature deuterophlebiid larvae, including thoracic spines (in some species), transverse meso- and metanotal bands, and ventrolateral abdominal spines. Unlike most pupal cuticle, which remains pale and soft for ca. one hour after ecdysis (Kennedy 1958), the above macrosculptural features are dark and heavily sclerotized at ecdysis, apparently because of pre-hardening of cuticle. I have hypothesized (Courtney *in press 2*) that these structures are pre-hardened because of their utility either during (*re.* thoracic spines and mesonotal bands) or immediately after (*re.* mesonotal and metanotal bands, and ventrolateral abdominal spines) ecdysis.

Pre-hardening of pupal cuticle is apparently quite rare and, when it does occur, is usually associated with thoracic respiratory organs. With regard to the latter, the Deuterophlebiidae and Blephariceridae are not unusual (see character 41). However, deuterophlebiids are apparently unique in possessing several additional pre-hardened structures, some of which are otherwise lacking in Nematocera (*e.g.*, thick, transverse, thoracic bands and ventrolateral abdominal spines).

3.5.8.3 Adult

Character 28. *primary ocelli present (plesiotypic) / primary ocelli absent (apotypic).*

As discussed above (*re.* Nymphomyiidae), the plesiotypic state is characteristic of most Diptera, including the Blephariceridae. The apotypic state also occurs in several

Nematocera, including Deuterophlebiidae and Nymphomyiidae. I consider loss of primary ocelli a weak synapotypy of the Deuterophlebiidae, and assume convergent loss of ocelli in the Nymphomyiidae.

Character 29. *mouthparts and digestive tract well-developed (plesiotypic) / mouthparts and digestive tract predominantly atrophied (apotypic).*

Mouthpart and digestive tract reduction in the Deuterophlebiidae are undoubtedly correlated with the brief imaginal life (see chapter 5). Adult mouthparts (Figs. 4.31, 4.32, 4.55-4.57) consist primarily of a large, simple cibarial opening, with no evidence of articulated mouthparts. Internally, the digestive tract is almost completely atrophied, represented mostly by vestiges of Malpighian tubules. As discussed earlier (*re.* Nymphomyiidae), mouthpart and digestive tract reduction, aphagia, and a brief life are characteristic of the adults of some other Diptera, most notably the Nymphomyiidae and certain Chironomidae. It is assumed that these similarities are convergent.

Character 30. *wings remain attached throughout adult life (plesiotypic) / wings deciduous, shed after flight and/or during oviposition activities (apotypic).*

As in the Nymphomyiidae (see earlier), post-emergence loss of wings is characteristic of female Deuterophlebiidae and is related to oviposition behaviour (see chapter 5). I consider the ability to shed the wings an apotypic state, but assume it has evolved independently in the Deuterophlebiidae and Nymphomyiidae.

Character 31. *femur uniformly sclerotized, undivided (plesiotypic) / femur subdivided by apparently membranous cuticle into short, basal zone and elongate, distal zone (apotypic).*

The presence of a subdivided adult femur is considered a derived feature of the Deuterophlebiidae. As discussed earlier (*re.* Nymphomyiidae), similarities between the femoral structure of Deuterophlebiidae and Nymphomyiidae are probably the result of convergence, and reflect constraints of the pupal case and brief adult life (see Courtney *in press* 2).

Character 32. *spiracles present on abdominal pleurites (plesiotypic) / abdominal spiracles absent (apotypic).*

As discussed earlier (*re.* Nymphomyiidae), the absence of abdominal spiracles is considered an apotypic, but convergent, feature of Deuterophlebiidae and Nymphomyiidae.

Character 33. *spermathecae present, usually three in number (plesiotypic) / spermathecae absent (apotypic).*

As discussed above (*re.* Nymphomyiidae), the plesiotypic state is characteristic of many Diptera, including most Blephariceridae. The apotypic state occurs in relatively few taxa, including the Deuterophlebiidae and Nymphomyiidae. Although this regressive character is considered apotypic for each of these two families, I assume the similarity is convergent, and related to comparable life histories (*i.e.*, the brief imaginal life).

Character 57. *male antennal flagellum of seven or more articles, with distal-most article not markedly elongate (plesiotypic) / male antennal flagellum of four articles, with distal-most article comprising ca. 90% of total antennal length (apotypic).*

One of the most striking features of male Deuterophlebiidae is an extremely elongate antenna, the length of which consists mostly of the distal-most, fourth flagellomere. As discussed elsewhere (Courtney *in press* 2), this feature may be related to swarming or flying in close proximity to turbulent streams. No other Diptera demonstrates a comparable antennal arrangement, and this is clearly an autapotypy of the Deuterophlebiidae.

Character 58. *male acropod bearing a setiform empodium set with simple macrotrichia, and a pair of well-developed tarsal claws (plesiotypic) / male acropod bearing a broad empodium set with dense capitate macrotrichia, and vestigial tarsal claws (apotypic).*

The acropod of a male deuterophlebiid is unique among Nematocera, consisting of a markedly broadened empodium bearing only the vestiges of tarsal claws. As discussed elsewhere (Courtney *in press 2* and chapter 5), male imagos are incapable of terrestrial activity (*i.e.*, walking), and spend their entire life in flight. Male activity, which is usually concentrated above whitewater or turbulent streams, often results in individuals being knocked into the water. The modified male acropod, with the broad empodium bearing dense capitate macrotrichia, may provide a snowshoe effect; *i.e.*, it may prevent imagos that are knocked to the stream from breaking through the surface tension, thereby allowing the fly to quickly resume flight. Although a few other Diptera lack tarsal claws (see Courtney *in press* 2), none exhibit the same acropod structure as mountain midges, with the latter clearly autapotypic of the Deuterophlebiidae.

3.5.9 Family Blephariceridae - Groundplan Apotypies

3.5.9.1 Larva

Character 8. *labrum dorsoventrally flattened (plesiotypic) / labrum laterally compressed, conical or wedge-shaped (apotypic).*

As discussed above (re. Psychodomorpha), the apotypic state has probably evolved independently in the Blephariceridae, Thaumaleidae, and in most Psychodomorpha.

Character 11a. *abdominal segments I to VII each with a pair of elongate, eversible, crochet-tipped, lateral prolegs (plesiotypic) / lateral prolegs vestigial on abdominal segment VII, and all prolegs lacking eversible crochets in instars II-IV (apotypic).*

Wood and Borkent (*in press*) and I (Courtney *in press 1*; earlier in this chapter) have argued that the Blephariceromorpha larval groundplan included eversible, crochet-tipped, lateral abdominal prolegs. In Blephariceridae, prolegs are present in instar I larvae of the subfamily Blepharicerinae, on only the cephalothorax (= abdominal segment I) and each of abdominal segments II-VI. As discussed earlier, I consider the loss of lateral prolegs on abdominal segment VII, and modifications of the remaining prolegs (*i.e.*, loss of eversible crochets) in instars II-IV, as apotypic and part of a transformation series.

Character 11b. *instar I cephalothorax and each of abdominal segments II-VI with a pair of eversible, crochet-tipped, lateral, abdominal prolegs (plesiotypic) / eversible, crochet-tipped, lateral, abdominal prolegs vestigial in instar I (apotypic).*

As discussed earlier, the presence of eversible, crochet-tipped prolegs is thought to be a groundplan feature of the Blephariceromorpha. Lack of eversible prolegs in the blepharicerid subfamily Edwardsininae is, therefore, considered secondarily derived, and part of the above-described (*re*. Blephariceromorpha) transformation series.

Character 38a. *head and thorax indistinguishably fused in early instars (plesiotypic) / head, thorax, and abdominal segment I fused (= cephalothorax) in all instars (apotypic).*

I have argued (re. Blephariceroidea) that this character involves a transformation series, with the plesiotypic state (as listed here) representing the intermediate condition, and a weak indicator of the monophyly of the Blephariceroidea. The final stage of this presumed transformation, the fusion of the head, thorax, and first abdominal segment, is one of the most distinctive and unique features of the Blephariceridae.

Character 55. *genae ventromedially extended and united to form a postgenal bridge (plesiotypic) / genae ventromedially separated, not forming a postgenal bridge (apotypic).*

As discussed earlier (*re.* Deuterophlebiidae), I consider lack of a postgenal bridge in Deuterophlebiidae and many Blephariceridae (subfamily Blepharicerinae) to be convergent, and due to desclerotization of a previously fused ventral cranium. Information on the cranial structure of early instar Edwardsininae will provide a test for this phylogenetic interpretation (see Courtney *in press 1*).

Character 59. *frons and clypeus indistinguishably fused, forming a cephalic apotome (plesiotypic) / cephalic apotome divided by a band of membranous cuticle ("frontoclypeal" suture) (apotypic).*

Although this character and character 34 may be related, I have chosen to treat them separately. The plesiotypic condition is characteristic of most Nematocera, including the Nymphomyiidae and most Psychodomorpha. Deuterophlebiidae demonstrate a rather different arrangement, with all dorsal and lateral cranial sclerites indistinguishably fused (*i.e.*, in instars II-IV; see character 47). In only the Blephariceridae (Anthon and Lyneborg 1968) and some Bibionidae (Teskey 1981) is the cephalic apotome divided by a "frontoclypeal" suture. As discussed elsewhere (Courtney *in press 1*), I assume that this suture is not part of the Diptera groundplan, nor is it homologous to the frontoclypeal suture of other insects (*e.g.*, Mecoptera). The presence of a divided cephalic apotome in Bibionidae, but not in most members of the Bibionomorpha (*sensu* Wood and Borkent *in press*), suggests that the bibionid condition is not homologous to that in Blephariceridae. I assume this to be the case, and consider that a divided cephalic apotome is an autapotypic feature of each family.

Character 60. *abdominal segments without suction devices (plesiotypic) / cephalothorax and abdominal segments II-VI each bearing a ventral suction device (apotypic).*

The presence of ventral suction devices is perhaps the most distinctive feature of larval Blephariceridae. Similar attachment devices occur on the larvae of certain Psychodidae (*i.e.*, *Maruina*), and the evolution of these structures may have been similar in both groups (Tonnoir 1933); however, the suction devices of *Maruina* and those of the Blephariceridae are clearly not homologous. Wood and Borkent (*in press*) held a similar view, and listed the presence of ventral suction devices as an apotypy of Blephariceridae.

Character 61. *tracheal gills absent (plesiotypic) / tracheal gills on anteroventral margins of abdominal segments II-VI in later-instar (II-IV) larvae (apotypic)*[1].

Tracheal gills[2] are found only in the Blephariceridae and some Chironomidae. In the latter group, tracheal gills (= "ventral tubules" *sensu* Saether 1977) are in the form of 1-2 pair of elongate, simple lobes on abdominal segment VIII; these structures are clearly of independent origin to the tracheal gills of Blephariceridae. In blephariceridss, tracheal gills usually consist of a pair of simple (instar II) of multi-lobed (instars III-IV) structures on the anteroventral margins of abdominal segments II to VI. The presence and structure of these gills is an autapotypy of the Blephariceridae.

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[1] In certain Blephariceridae (*e.g.*, *Philorus californicus* Hogue), tracheal gills may be apparent only in instar IV larvae.

[2] Unlike anal papillae, which are sometimes incorrectly called "tracheal giils", tracheal gills apparently function primarily as respiratory organs (Harnisch 1954; Whitton 1963).

Character 62. *Malpighian tubules arising separately and more or less equidistantly around periphery of gut (plesiotypic) / Malpighian tubules borne on a pair of lateral stalks (with a 2+3 or 3+2 arrangement) (apotypic).*

Outside of the Bibionomorpha, stalked Malpighian tubules are relatively uncommon in Diptera (see Table 2). With regard to the origin and proximal arrangement of tubules, I assume that the Deuterophlebiidae are plesiomorphic; *i.e.*, tubules arise separately and more or less equidistantly around the periphery of the gut. In Blephariceridae, the five tubules are borne on a pair of laterally situated stalks, with two tubules on the left stalk and three on the right stalk (*personal observation*; Zwick 1977); the reverse (*i.e.*, three on left, two on right), or both arrangements are demonstrated by some taxa (*personal observation*). Although the Malpighian tubules of Nymphomyiidae are rather unusual and borne on a common stalk (see character 18), I consider their structure non-homologous to that in Blephariceridae. I consider the blepharicerid condition to be autapotypic for the family.

3.5.9.2 Adult

Character 14a. *empodium setiform (plesiotypic) / empodium vestigial (apotypic).*

I proposed earlier that the Blephariceromorpha groundplan included a setiform empodium, and that this structure has been lost in the Blephariceridae as the last step of a transformation sequence. I assume a convergent arrangement in the Tanyderidae.

Character 63. *aedeagus with a single, terminal opening, corresponding to a single opening of a common spermathecal duct in the female, formed by the union of three spermathecal ducts (plesiotypic) / aedeagus with three, long, slender filaments, each with a separate opening, corresponding to three, separate spermathecal duct openings in the female (apotypic)* — (Wood and Borkent *in press*).

The Blephariceridae, Tanyderidae, and some Tipulidae possess a trifid aedeagus, a feature Downes (1968) considered plesiotypic for Diptera. However, neither Mecoptera nor Siphonaptera demonstrate this arrangement (Downes 1968), and it seems more likely that a trifid aedeagus is derived. Wood and Borkent (*loc. cit.*) proposed that the trifid aedeagus was apotypic for the Blephariceridae, and suggested that the arrangement evolved independently in other groups. I concur with this interpretation.

3.5.10 Character States of Undetermined Polarity [Adult]

thoracic sternites large, exposed. — According to McAlpine (1981), certain of the Blephariceromorpha demonstrate unique thoracic features. In most Diptera, both the meso- and metasternum are predominantly invaginated. However, the mesosternum is relatively large and exposed in Nymphomyiidae, Deuterophlebiidae, and some Blephariceridae, Tipulidae, and Anisopodidae. The metasternum is also partly exposed in Nymphomyiidae and Deuterophlebiidae. It is unclear if these features are plesiotypic or apotypic.

prescutal suture. — A prescutal suture occurs in the Tipulidae, Blephariceridae, Psychodidae, Axymyiidae (McAlpine 1981) and Deuterophlebiidae (Courtney *in press* 2). Again, it is unclear if this is a plesiotypic or apotypic feature.

wing base broad. — Hennig (1973) speculated that the broad wing base in the Deuterophlebiidae, Blephariceridae, and Simuliidae was an adaptation of stream-inhabiting flies that pupate beneath the water. He predicted that a broad wing base would permit rapid emergence and unfolding of wings upon reaching the stream surface. While this would seem a compelling feature and potential synapotypy of the Blephariceroidea, I fail to appreciate its applicability to the Blephariceridae. With few exceptions (*e.g.*, *Bibiocephala*, *Hapalothrix*), the blepharicerid wing base does not appear to be markedly broad, and I am unable to see the basis for which Hennig included the Blephariceridae in this discussion. An alternate, and perhaps more likely, explanation of the broad wing base (and anal lobe) may be found in swarming and mating behaviour (McAlpine and Munroe 1968).

pulvilli absent. — Pulvilli are lacking in the Tipulomorpha, Blephariceromorpha, Psychodomorpha (except Perissommatidae), Ptychopteromorpha, and most Culicomorpha. These structures are present in Axymiomorpha, Bibionomorpha (except Mycetophilidae), and some Culicomorpha. The absence of pulvilli is likely plesiotypic, particularly since this arrangement is typical of the Mecoptera (Hennig 1973).

gonocoxites and hypandrium fused into a single sclerite. — Wood and Borkent (*in press*) proposed fusion of the gonocoxites and hypandrium as a synapotypy of the Blephariceroidea. In addition to the Blephariceridae[1] and Deuterophlebiidae, this feature is typical of several Nematocera, including Axymyiidae (Wood 1981), and some Tipulidae, Simuliidae, and Bibionidae (Wood and Borkent *loc. cit.*). Mecoptera also demonstrate this arrangement. I am not convinced of the polarity decision of Wood and Borkent (nor were they!), and do not consider fusion of the gonocoxites and hypandrium a synapotypy of the Blephariceroidea.

aedeagal sheath. — The aedeagus is sheathed (at least basally) in all members of the Blephariceromorpha, and this arrangement may represent a synapotypy of the infraorder. However, the homologies of the aedeagal sheath are unclear, and a source of considerable disagreement (Griffiths 1989, *personal communication*). In the Blephariceromorpha, the fundamental problem is marked reduction of genitalic appendages in Nymphomyiidae and Deuterophlebiidae. Both groups have relatively simple genitalia, consisting essentially of an epandrium, sheathed aedeagus, and pair of gonopods (which may or may not be fused with the hypandrium). In contrast, Blephariceridae have apparently retained most of the basic genitalic appendages, and homologies of the aedeagal sheath can be determined with some certainty. The base of the aedeagus is surmounted by the plate-like tegmen, and each aedeagal filament is further housed in a separate sheath (the latter of which presumably represents part of the aedeagus (Griffiths 1989, *personal communication*)). It is unknown if the nymphomyiid or deuterophlebiid aedeagal sheath are formed in a similar manner.

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[1] The fused gonocoxites and hypandrium referred to as the "genital capsule" by Hogue (1987).

3.6 Zoogeographic Considerations

The distributions of the Nymphomyiidae, Deuterophlebiidae, and Blephariceridae include a relatively large area, and parts of all major continents (Fig. 5); however, the former two taxa are presently restricted to the northern hemisphere. Disjunct distributions are the norm, presumably reflecting the locations of mountainous areas. Both the Nymphomyiidae and Deuterophlebiidae are exclusively Holarctic, with nymphomyiids known from the Himalaya, eastern Palaearctic and eastern Nearctic Regions, and deuterophlebiids from mountains of the central and eastern Palaearctic and western Nearctic Regions. In contrast, the Blephariceridae, particularly the subfamily Blepharicerinae, are much more widespread, occurring on all major land masses. The blepharicerid subfamily Edwardsininae has a seemingly Gondwanian distribution, with all extant species from the southern hemisphere.

Perhaps because of their torrenticolous habitat, and the likelihood that moribund individuals are abraded and destroyed by the current, Nymphomyiidae, Deuterophlebiidae, and Blephariceridae are sorely lacking in the fossil record. Fossil data are summarized in Figure 6, which shows superposition of the Nematocera[1] phylogeny, geological time scale, and fossil records (based primarily on Hennig 1981). Although the oldest known Diptera fossils are from the Upper Triassic, it is generally assumed that the ancestral dipteran stock was present by the Permian (Hennig 1981); however, the timing of dichotomies shown in Figure 6 is rather arbitrary between the Permian and Upper Triassic (the same is true for basal dichotomies of the Blephariceromorpha). Fossils are unknown for both nymphomyiids and deuterophlebiids. Fossil blepharicerids, including representatives of both subfamilies, were discovered recently in the far eastern Soviet Union (Kovalev 1987)[2]; these fossils are apparently from the Cenomanian, or near the beginning of the

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[1] The suborder Nematocera, as recognized here and by most dipterists, is probably not monophyletic, but a grade-level taxon. The suborder Brachycera, or the so-called "higher flies", probably evolved from one of the nematocerous clades, possibly either the Bibionomorpha or Psychodomorpha.

[2] I have seen neither specimens nor figures of this material; Kovalev evidently was confident enough with the determination to place a genus name on the Edwardsininae fossils (*Paulianina*).

Upper Cretaceous. Discovery of Edwardsininae fossils in the northern hemisphere supports the hypothesis (Stuckenberg 1958; Zwick 1977) that the group's exclusively southern contemporary distribution is relictual.

If we accept the reconstructed phylogeny and fossil data, the Blephariceromorph line must have diverged from the Psychodomorph line no later than the Upper Triassic. Thus both lineages are at least of Pangean age. Fossils indicate that the Blephariceridae diverged into two subfamilies before the Upper Cretaceous; thus, divergence of both the ancestral nymphomyiid and deuterophlebiid must have pre-dated this, and probably by a substantial margin. Most extant members of the Blephariceromorpha are torrenticolous specialists, and the ancestral Blephariceromorph probably inhabited montane, running-water habitats, as well. The tectonic and orogenic activity subsequent to the breakup of Pangea should have provided considerable opportunity for diversification of these stream insects, but only the Blephariceridae seem to have capitalized on this opportunity. The Nymphomyiidae and Deuterophlebiidae are neither speciose nor widespread, and it seems evident that both are relict taxa.

3.7 Phylogenetic Conclusions

Cladistic analysis of more than 60 characters has tested the phylogenetic hypotheses of Rohdendorf (1974), Hennig (1973), Wood and Borkent (*in press*) and Courtney (*in press 1*). Analysis of features of larval, pupal, and adult Diptera supports the phylogeny of Wood and Borkent, as modified by Courtney (*loc. cit.*). Monophyly of the Blephariceromorpha (Nymphomyioidea + Blephariceroidea) was supported by one adult and five larval characters. Substantially more evidence for monophyly of the Blephariceroidea (Deuterophlebiidae + Blephariceridae) has been provided, with the clade now defined by synapotypic characters of the larva (six), pupa (three) and adult (four). Synapotypies were given to further support monophyly of each of the Nymphomyiidae, Deuterophlebiidae, and Blephariceridae. Several convergences between deuterophlebiids and nymphomyiids were identified, most (*e.g.*, vestigial mouthparts and digestive system) presumedly reflecting independent evolution of a short-lived, non-feeding, imaginal stage.

This analysis has also helped resolve the 4-way polytomy (one lineage of which was the Blephariceromorpha) of the Wood and Borkent reconstruction. Larval structures suggest that the Blephariceromorpha and Psychodomorpha form a monophyletic group. Superficially, this may seem a return to the classification of Hennig (1973); however, in terms of the familial composition of Psychodomorpha, there is little similarity between the Hennig, and Wood and Borkent classifications (*cf.* Figs. 2, 3).

Although the reconstructed phylogenies of Wood and Borkent and the present analysis are perhaps the "best-supported" of any in existence, neither is without problems or equivocal groups. The system proposed by Wood and Borkent, and accepted in the present study, places considerable weight on features of the larval mandible. For certain of these characters (*e.g.*, structure of the basal mandibular lobe), the substantial weights would seem justifiable; however, arguments for the significance of other character states (*e.g.*, oblique to vertical mandibular rotation as a synapotypy of the Blephariceromorpha, Psychodomorpha, Ptychopteromorpha and Culicomorpha) seem less compelling. Wood and Borkent considered that shifts in mandibular rotation may reflect larval habitat and feeding behaviour, and apparently they were willing to accept several reversals on these grounds. However, the prevalence of reversals suggests that the character is subject to homoplasy and of questionable phylogenetic value. Further investigations of the structure and distribution of mandibular characters are warranted, and may provide valuable insights into the phylogenetic relationships. Unfortunately, few detailed, comprehensive studies of Diptera mandibles, or other mouthparts (*e.g.*, maxillae), have been done, and data for some taxa are almost non-existent. Among the latter is the Nymphomyiidae.

At present, several important character states, including three of the four that define the Blephariceromorpha + Psychodomorpha, have not been definitively determined for the

Nymphomyiidae. A detailed investigation of nymphomyiid larval mouthparts and cranial structure is needed and, until such a study is conducted, the placement of nymphomyiids remains equivocal. However, if the Nymphomyiidae is eventually moved out of the Blephariceromorpha and re-rooted in the phylogeny, it seems likely that the family will be placed in a more derived clade, rather than toward the base of the Diptera. As discussed earlier, support for the latter hypothesis is based mostly on character states that could reflect neoteny, rather than plesiotypy. Some nymphomyiid features suggest affinities with certain Culicomorpha; however, until a detailed, morphological study of nymphomyiids is conducted, the significance of these similarities remains unclear.

One of the most difficult problems faced by students of Diptera phylogenetics is general lack of knowledge about early-instar larvae. Several crucial synapotypies, particularly in the Blephariceromorpha, pertain to first instars. Data for first instars are available for many Culicomorpha and, as the result of this research, for deuterophlebiids and blephariceridae; in all instances, information about early instars provides valuable insights into phylogenetic relationships. Unfortunately, early instars are inadequately known for many other groups, including nymphomyiids and most Psychodomorpha.

In spite of these problems, substantial evidence supports a sister group relationship between the Deuterophlebiidae and Blephariceridae; therefore, polarity decisions for phylogenetic analyses of species of the Deuterophlebiidae (see chapter 6) can assume the Blephariceridae are the immediate outgroup of deuterophlebiids.

It is apparent that there are huge gaps in knowledge about Diptera phylogeny. This investigation of the Deuterophlebiidae has partly filled one of these gaps, and identified others of potential importance. Detailed morphological studies of early-instar larvae, particularly of groups such as the Nymphomyiidae, are needed and will be invaluable for deciphering the evolutionary history of Diptera. This analysis of the Blephariceromorpha hopefully will provide the impetus and basis for future studies of this taxon and other flies.

Table 1. Matrix of characters analyzed for evidence of monophyly and familial relationships of Blephariceromorpha
"0" = plesiotypic "2","3" = apotypic (i.e., subsequent stages in transformation sequences)
"1" = apotypic "?" = character state unknown "-" = not applicable

Taxon/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
Tipulidae	0/2	0	0	0/1	0	0	0?	0	0?	0	0	0/1	0	0	1	1	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Nymphomyiidae	?	1	1	?	?	?	-	0	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Deuterophlebiidae	1	1	0/1	1	1	1	-	0	1	1	1	1	1	1	0	-	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1
Blephariceridae	1	1	1	0/1	1	1	-	1	1	1	2/3	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psychodidae	1	0/1	1	1	1	0	1	1	0	0/1	0	0	0	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0/1
Trichoceridae	1	1	1	1	1	1	1	1	0	0	0	0	-	0	0	0	-	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
Perissommatidae	?	1	1	?	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
Anisopodidae	1	1	1	1	1	1	1	1	0	0	0	0	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Scatopsidae	1	1	1	1	1	1	1	1	0	0	0	0	-	0	1	?	-	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0
Synneuridae	?	?	?	?	?	?	?	?	?	?	0	0	-	0	?	?	-	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0
Tanyderidae	2	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0/1	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Ptychopteridae	1?	0	0	1	0	0	0	0	0	0	0	0	0?	0	0	0/1	-	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0
Dixidae	2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	-	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0
Chaoboridae (s. lato)	2	0	1	0	0	0	0	0	1	0	0	0/1	1	1	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Culicidae	2	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Thaumaleidae	2	1	1	0	0	0	0	1	0	0	0	0	0	1	1?	1	-	0	0	0	0	?	0	0	0	0	0	1	0	0	0	0
Simuliidae	2	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1	-	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Chironomidae	2	0/1	1	0	0	0	0	0	0	0	0	0/1	0	1	0/1	1	-	0	0/1	0	0	0	0	0	1	0/1	0	1	0/1	0	0	0
Ceratopogonidae	2	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	-	0/1	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Axymyiidae	2	0	0	0	0	0	0?	1	0?	0	0	0	1	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachyneuridae	2	0	0	0	0	0	0?	0	0?	0	0	0	-	0	0	0	-	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
Bibionidae	2	0	0	0	0	0	0?	0	0?	0	0	0	-	0	0	0	-	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0
Mycetophilidae	2	0	0	0	0	0	0?	0	0?	0	0	0/1	-	0	1	0	-	0	0	0	0	?	0	0	0/1	0	0	0/1	0	0	0	0
Cecidomyiidae	2	0	0	0	0	0	0?	0	0?	0	0	0	-	0	1	0	-	0	0	0	0	1?	0	0/1	0/1	0	0	0/1	0/1	0	0	0
Sciaridae	2	0	0	0	0	0	0?	0	0?	0	0	0	-	0	1	0	-	0	0	0	0	?	0	0	0/1	0	0	0	0	0	0	0

Table 1 (ctd). Matrix of characters analyzed for evidence of monophyly and familial relationships of Blephariceromorpha
"0" = plesiotypic "2","3" = apotypic (i.e., subsequent stages in transformation sequences)
"1" = apotypic "?" = character state unknown "-" = not applicable

Taxon/Character	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Tipulidae	0	0	0	0	1	0/1	0	0	0/1	0	0/1	0	0	0	0/1	0	0	1?	0/1	-	0	0	0/1	0	0	0	0	0	0	0	0/1
Nymphomyiidae	**1**	**?**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**?**	**?**	**?**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Deuterophlebiidae	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Blephariceridae	**0**	**1**	**1**	**1**	**1**	**2**	**1**	**1**	**2**	**1**	**1**	**1**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0/1**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**1**
Psychodidae	0	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0/1	0	0	0
Trichoceridae	0	?	0	0	0	0	0	0	0	0	0	0	0	1?	0	0	0	?	0	-	-	-	0	0	0	0	0	0	0	0	0
Perissommatidae	0	?	0	0	?	0	?	0	0	0	1	0	0	0	0	0	?	?	?	-	0	0	0	0	0	0	0	0	0	?	0
Anisopodidae	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	0	-	-	-	0/1	0	0	0	0	0	0	0	0
Scatopsidae	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	-	-	-	0	0	0	0	0	0	0	0	0
Synneuridae	0	?	0	1	-	?	0	0	0	0	0	0	1	0	-	0	?	?	?	-	-	-	-	0	0	0	?	0	0	0	0
Tanyderidae	0	0	0	0	1	1	1	0	0/1	0	0	0	0	0	0/1	0	0	0	0	-	0	0/1	0/1	0	0	0	0	0	0	0	1
Ptychopteridae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0/1	0	0	0	0	0	0	0	0	0
Dixidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0
Chaoboridae (s. lato)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0
Culicidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0
Thaumaleidae	1?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0
Simuliidae	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	-	0	0	0	0	0	0	0	0	0	0	0
Chironomidae	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0/1	-	0	0	0	0	0	0	0	0	0/1	0	0
Ceratopogonidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0
Axymyiidae	0	?	0	0	?	1	0	0	0	0	1	0	1	1	0	0	0	?	0	-	0	0	0	0	0	0	0	0	0	0	0
Pachyneuridae	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?	?	1	-	-	-	0/1	0	0	0	0	0	0	1	0
Bibionidae	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	1	-	-	-	0/1	0	0	0	1	0	0	0/1	0
Mycetophilidae	0	?	0	?	0	0	0	0	0	0	0	0	1	0	0	0	?	?	1	-	-	-	0/1	0	0	0	0	0	0	0	0
Cecidomyiidae	0	?	0	?	0	0/1	0	0	0	0	0	0	0	0	0	0	?	?	1	-	-	-	0/1	0	0	0	0	0	0	0	0
Sciaridae	0	?	0	?	0	0	0	0	0	0	0	0	1	0	0	0	0	?	1	-	-	-	0/1	0	0	0	0	0	0	0/1	0

Table 2. Distribution and arrangement of Malpighian tubules in Diptera.

Family	# M. t.	Stalked	Reference(s)
Tipulidae	4	(-)	Krivosheina 1969; Zwick 1977; Byers 1983
Blephariceridae	5	(+)	*personal observation*; Zwick 1977
Deuterophlebiidae	5	(-)	*personal observation*; Pulikovsky 1924
Nymphomyiidae	2	(+)	*personal observation*; Tokunaga 1936
Psychodidae	5	(-)	Snodgrass 1935; Zwick 1977
Trichoceridae (*Trichocera*)	4	(-)	Zwick 1977
Perissommatidae	?	?	[no reference found]
Anisopodidae	4	(-)	Keilin and Tate 1940; Krivosheina 1969
Scatopsidae (*Scatopse*)	4	(-)	Madwar 1937
Synneuridae	4	(-)	Krivosheina 1969
Tanyderidae	5	(-)	*personal observation*
Ptychopteridae	5	(-)	Rohdendorf 1974
Dixidae (*Dixa*)	4	(-)	Zwick 1977
Chaoboridae	4	(-)	Staddon 1962
Culicidae	5	(-)	Thompson 1905; Snodgrass 1935
Thaumaleidae (*Thaumalea*)	4	(-)	Zwick 1977
Simuliidae	4	(-)	Rubtsov 1969; Zwick 1977
Chironomidae (*Chironomus*)	4	(-)	Credland 1981
Ceratopogonidae			
Forcipomyia	3	(-)	Lawson 1951
Culicoides	2	(-)	Lawson 1951
Axymyiidae	4	(-)	Mamayev and Krivosheina 1966
Pachyneuridae	4	(-)	Krivosheina and Mameyev 1970
Bibionidae (*Bibio*)	4	(+, -)	Madwar 1937; Krivosheina 1969
Mycetophilidae	4	(-)	Madwar 1937
Sciaridae	4	(+, -)	Madwar 1937; Krivosheina 1969
Cecidomyiidae			
Camplyomyza, Wyattella	4	(-)	Krivosheina 1969
Camptomyia	3	(-)	Krivosheina 1969
Harmandia	2	(-)	Krivosheina 1969
Brachycera	4	(+, -)	various sources

Figure 1. Phylogenetic relationships of Diptera, (Rohdendorf 1974).

Infraorders: 1 - Nymphomyiomorpha
2 - Deuterophlebiomorpha
3 - Blephariceromorpha
4 - Tipulomorpha
5 - Bibionomorpha

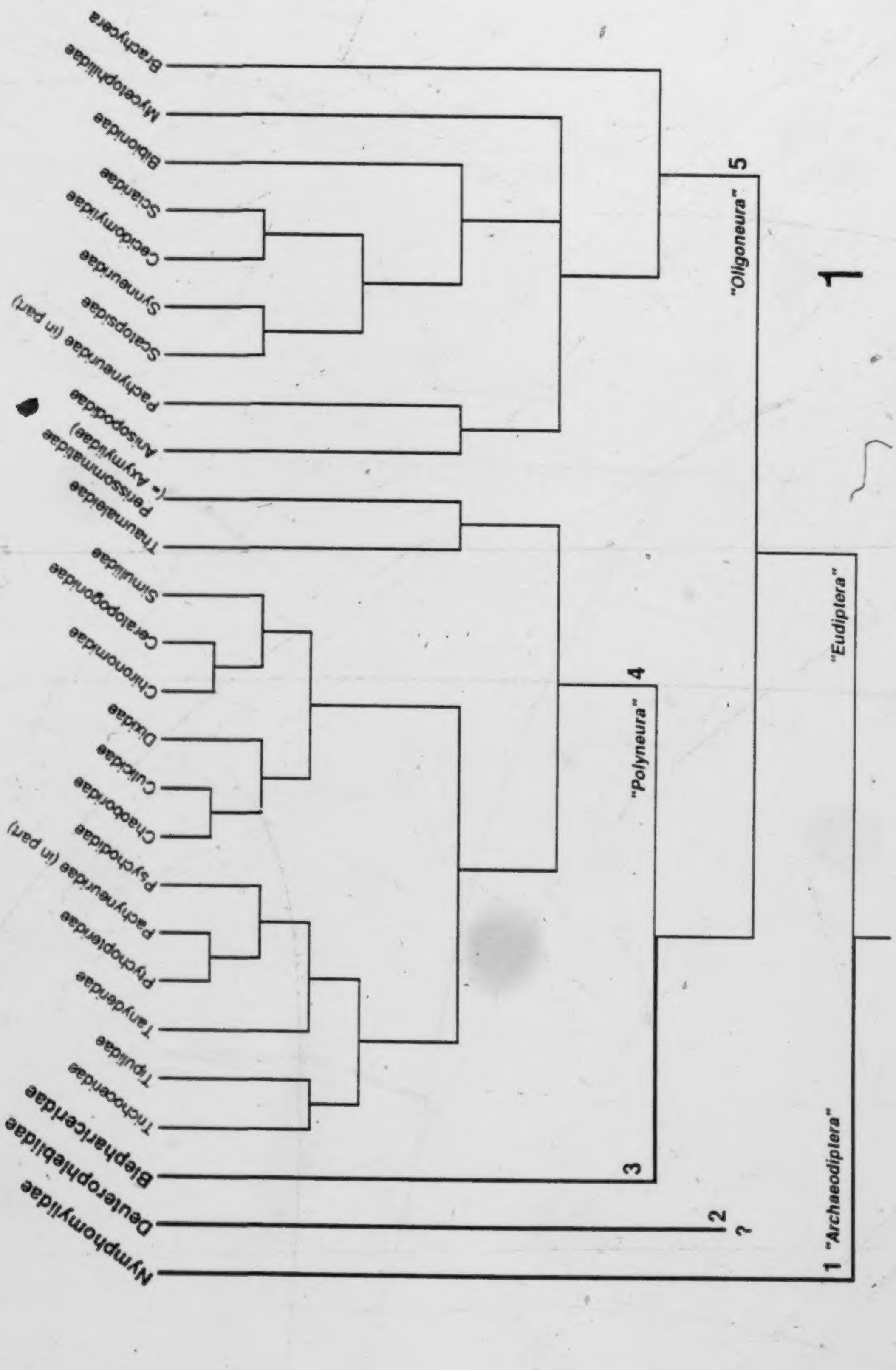
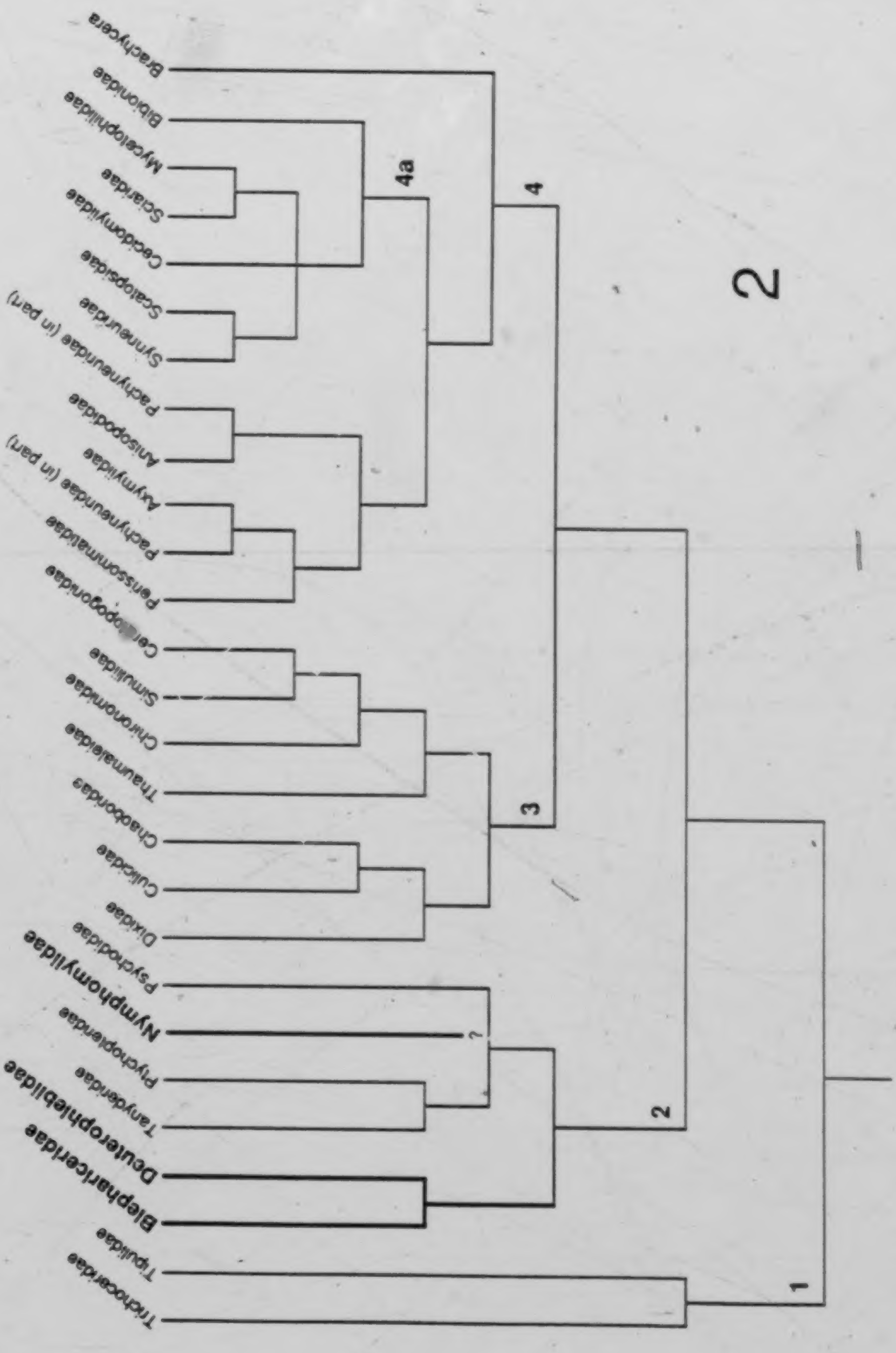

Brachycera
Mycetophilidae
Bibionidae
Sciaridae
Cecidomyiidae
Synneuridae
Scatopsidae
Pachyneuridae (in part)
Anisopodidae
(= Axymyiidae)
Perissommatidae
Thaumaleidae
Simuliidae
Ceratopogonidae
Chironomidae
Dixidae
Culicidae
Chaoboridae
Psychodidae
Pachyneuridae (in part)
Ptychopteridae
Tanyderidae
Tipulidae
Trichoceridae
Blephariceridae
Deuterophlebiidae
Nymphomyiidae
1 "Archaeodiptera"
2
?
3
4 "Polyneura"
5 "Oligoneura"
"Eudiptera"
1

Figure 2. Phylogenetic relationships of Diptera (Hennig 1973).

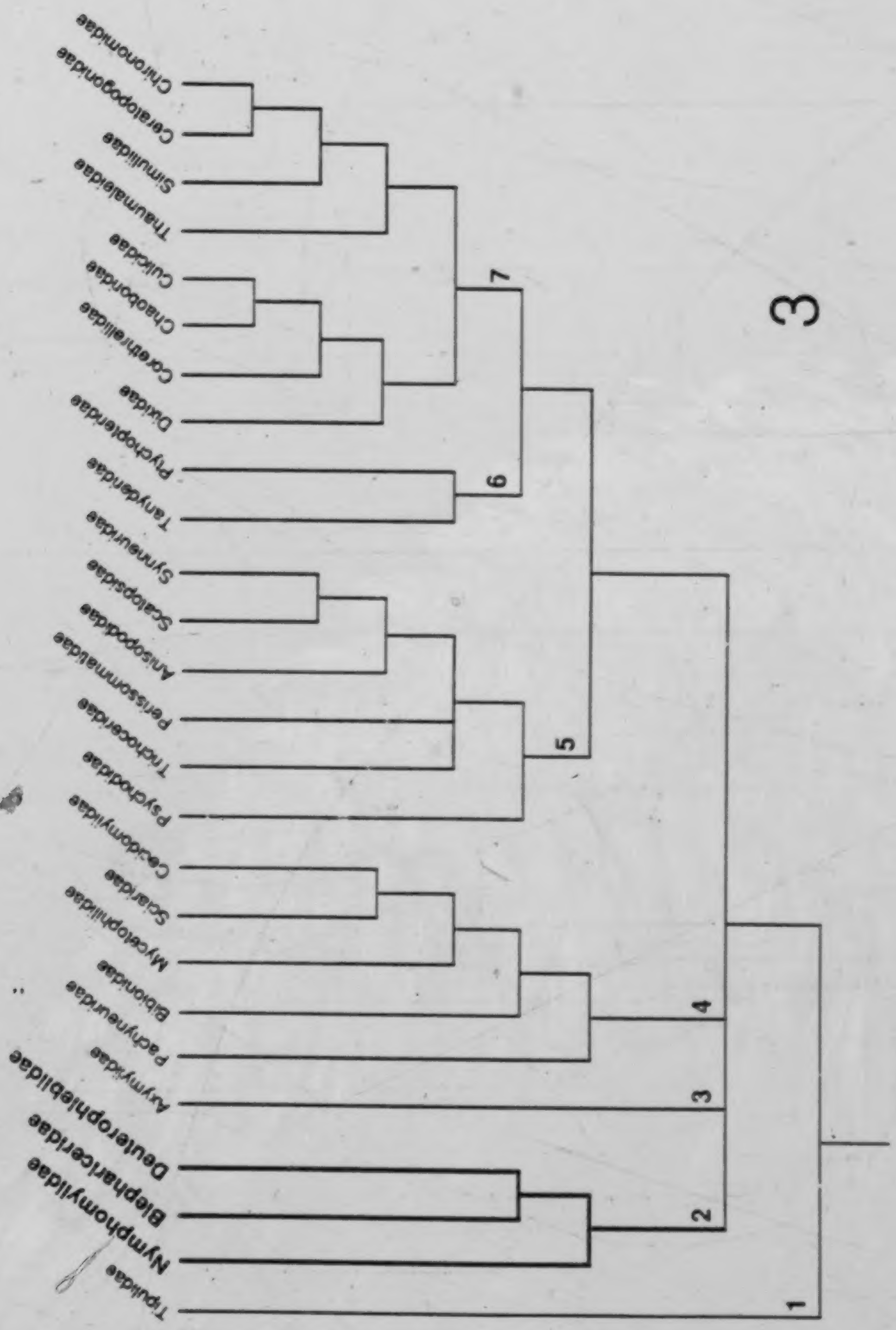
Infraorders: **1** - Tipulomorpha
2 - Psychodomorpha
3 - Culicomorpha
4 - Bibionomorpha (*sensu lato*)
4a - Bibionomorpha (*sensu stricto*)


Brachycera
Bibionidae
Mycetophilidae
Sciaridae
Cecidomyiidae
Scatopsidae
Synneuridae (in part)
Pachyneuridae
Anisopodidae
Axymyiidae
Pachyneuridae (in part)
Perissommatidae
Ceratopogonidae
Simuliidae
Chironomidae
Thaumaleidae
Chaoboridae
Culicidae
Dixidae
Psychodidae
Nymphomyiidae
Ptychopteridae
Tanyderidae
Deuterophlebiidae
Blephariceridae
Tipulidae
Trichoceridae
4a
4
3
?
2
1

2

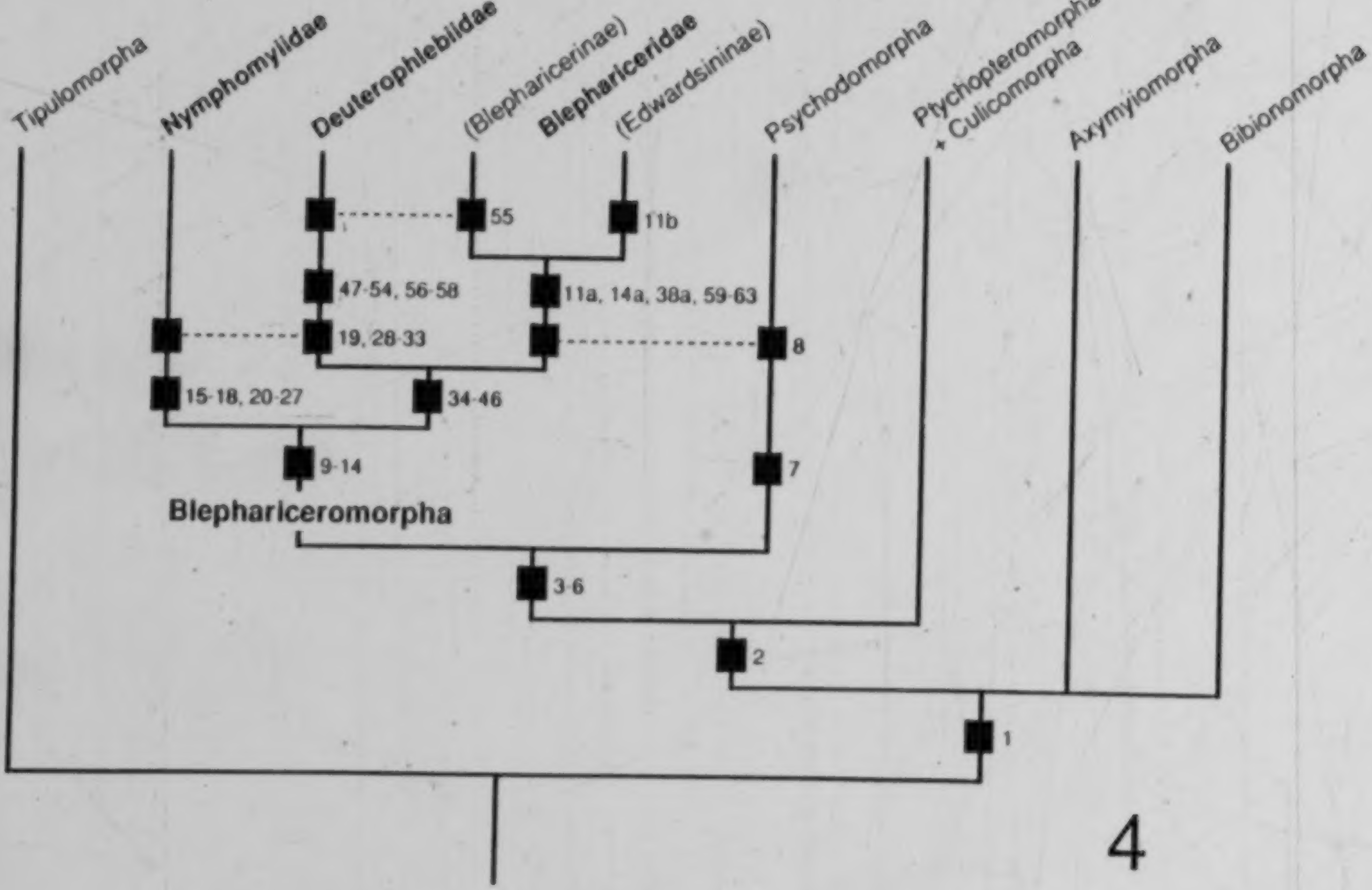
Figure 3. Phylogenetic relationships of Nematocera (Wood and Borkent *in press*).

Infraorders: 1 - Tipulomorpha
2 - Blephariceromorpha
3 - Axymiomorpha
4 - Bibionomorpha
5 - Psychodomorpha
6 - Ptychopteromorpha
7 - Culicomorpha


Tipulidae
Nymphomyiidae
Blephariceridae
Deuterophlebiidae
Axymyiidae
Pachyneuridae
Bibionidae
Mycetophilidae
Sciaridae
Cecidomyiidae
Psychodidae
Trichoceridae
Perissommatidae
Anisopodidae
Scatopsidae
Synneuridae
Tanyderidae
Ptychopteridae
Dixidae
Corethrellidae
Chaoboridae
Culicidae
Thaumaleidae
Simuliidae
Ceratopogonidae
Chironomidae
1
2
3
4
5
6
7

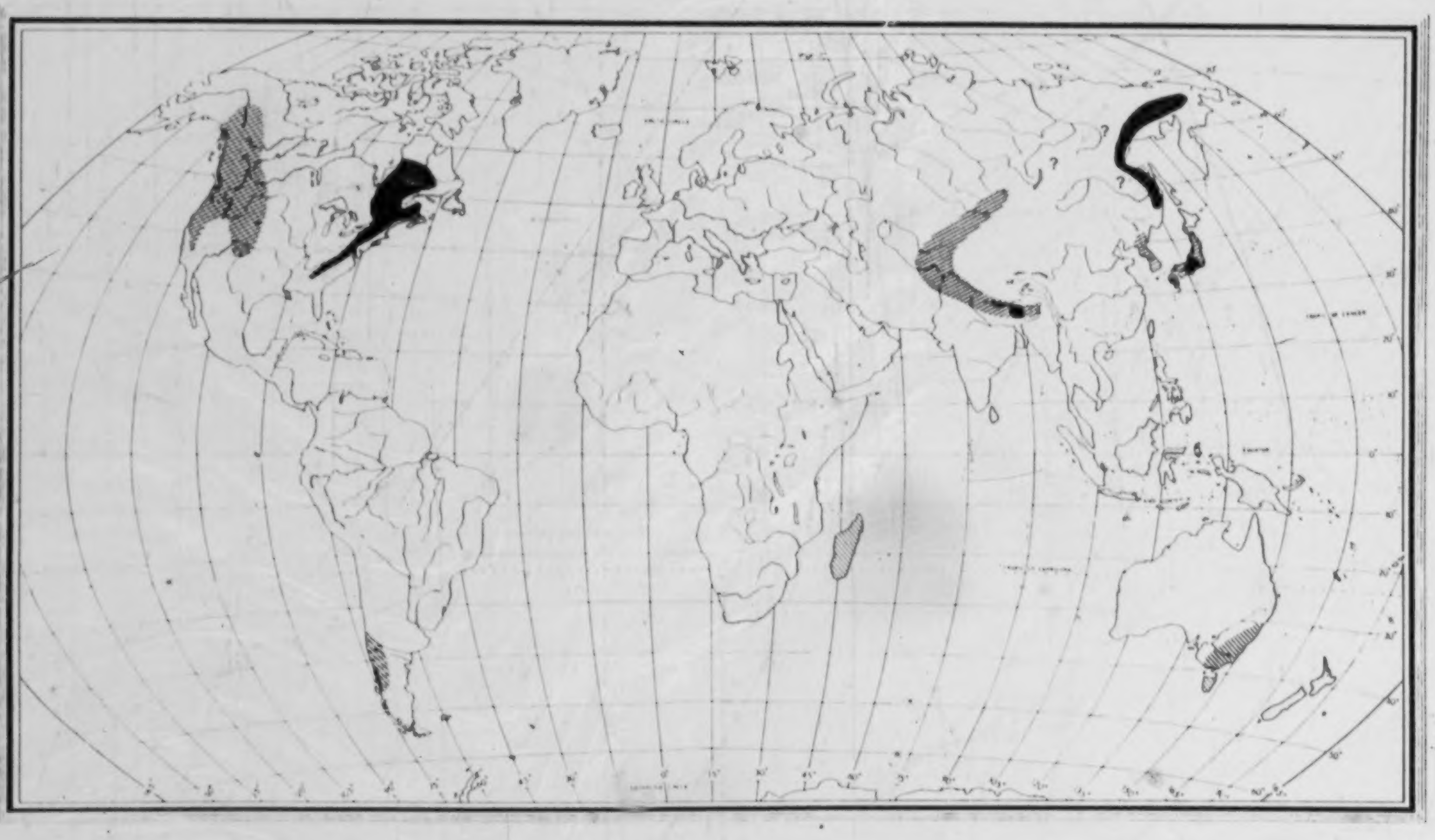
3

Figure 4. Hypothesized phylogenetic relationships of Blephariceromorpha and related Diptera. **Apotypies: 1**, mandibular lobe fused to base, prostheca arising from median surface of mandible; **2**, mandibular condyles displaced, rotation oblique to vertical; **3**, torma articulated with dorsal labral sclerite; **4**, mandible "biarticled"; **5**, mandibular epicondyle on tentorial phragma; **6**, cardo membranous; **7**, premandible an oval sclerite, with comb-like teeth; **8**, labrum laterally compressed; **9**, premandibles lacking; **10**, apex of mandible comb-like; **11**, abdominal segments I-VII with eversible, crochet-tipped, lateral prolegs; **11a**, prolegs vestigial on abdominal segment VII, and prolegs lacking eversible crochets in instars II-IV; **11b**, eversible, crochet-tipped, prolegs vestigial in instar I; **12**, apneustic; **13**, anal papillae nonretractable; **14**, empodium setiform; **14a**, empodium lost; **15**, larval tentorium rudimentary; **16**, postmentum anteriorly serrate and fused to postgenal bridge; **17**, prolegs with dimorphic crochets; **18**, two, stalked Malpighian tubules; **19**, labrum-epipharynx with spatulate macrotrichia; **20**, pupal head prognathous; **21**, compound eyes ventrally holoptic; **22**, adult tentorium vestigial; **23**, clavate flagellum with three flagellomeres; **24**, wing narrow, with marginal fringe of elongate macrotrichia and ill-developed anal lobe; **25**, wing veins costalized; **26**, imago neotenic; **27**, abdominal tergite VIII with prominent anterolateral tubercle; **28**, primary ocelli absent; **29**, adult mouthparts and digestive tract vestigial; **30**, wings deciduous; **31**, femur and/or tibia subdivided; **32**, abdominal spiracles absent; **33**, spermathecae absent; **34**, instar I frontal sclerite separated from clypeus by membranous cuticle; **35**, antenna lateral, comparatively distant from peristomal margin; **36**, postmentum membranous; **37**, cranium laterally excised or medially extended into prothorax, with zone of intermolt cuticle deposition; **38**, head and prothorax indistinguishably fused in early instars; **38a**, cephalothorax; **39**, five Malpighian tubules; **40**, pupa dorsoventrally flattened, attached to the substrate by ventrolateral adhesive discs, and with tergites darkly sclerotized and sternites membranous; **41**, pupal respiratory organ a multi-branched, pre-hardened, plastron-bearing spiracular gill; **42**, wing reaching final size and shape before emergence; **43**, meron as fully developed behind the midcoxa as the katepisternum in front of the midcoxa; **44**, wings, at rest, not folded over the abdomen; **45**, costal vein absent beyond wing apex; **46**, male terminalia dorsoflexed; **47**, cranium lacking ecdysial lines; **48**, antenna bifurcate; **49**, labrum partly operated by an intrinsic muscle; **50**, hypopharyngeal suspensorium anteriorly serrate in instar I; **51**, pharyngeal apparatus absent; **52**, proleg crochets with five uniformly sized teeth; **53**, five anal papillae; **54**, Malpighian tubules terminate in anal papillae; **55**, genae separate, not forming a postgenal bridge; **56**, pupa with pre-hardened thoracic bands and ventrolateral abdominal spines; **57**, male flagellum of four articles, with distal-most article markedly elongate; **58**, male acropod with a broad empodium and vestigial tarsal claws; **59**, cephalic apotome divided by membranous cuticle; **60**, cephalothorax and abdominal segments II-VI each with ventral suction device; **61**, tracheal gills on abdominal segments II-VI; **62**, Malpighian tubules borne on lateral stalks; **63**, aedeagus with three, separate, slender filaments, corresponding to three, separate, spermathecal duct openings in the female.


Tipulomorpha
Nymphomyiidae
Deuterophlebiidae
(Blephariceriinae)
Blephariceridae
(Edwardsininae)
Psychodomorpha
Ptychopteromorpha
+ Culicomorpha
Axymyiomorpha
Bibionomorpha
55
11b
47-54, 56-58
11a, 14a, 38a, 59-63
19, 28-33
8
15-18, 20-27
34-46
9-14
7
Blephariceromorpha
3-6
2
1

4

Figure 5. Contemporary world distribution of Nymphomyiidae, Deuterophlebiidae and Blephariceridae.



Nymphomyiidae ●

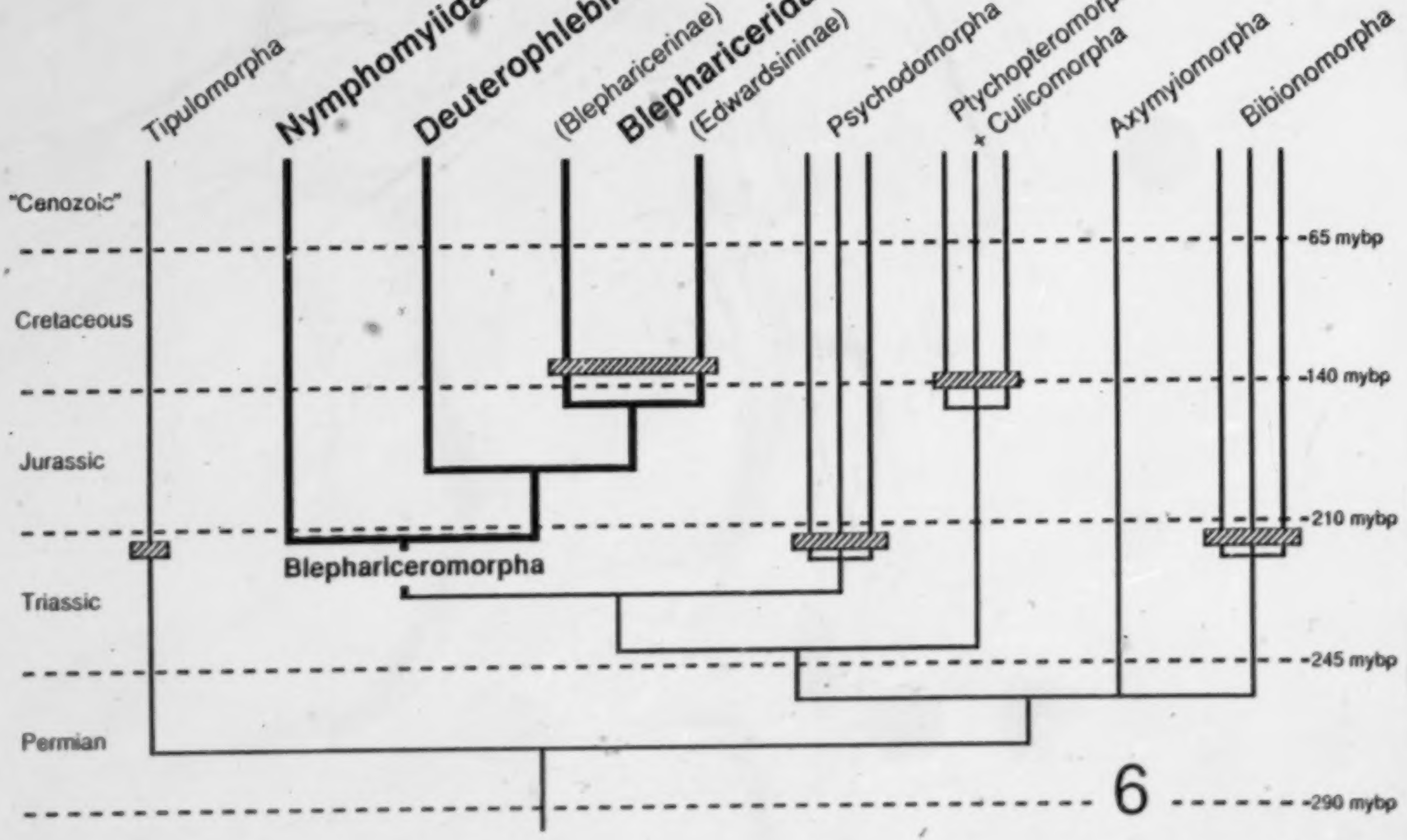
Deuterophlebiidae ▨

Blephariceridae (Blepharicerinae)

▨ (Edwardsininae)

5

Figure 6. Reconstructed phylogeny of Nematocera, in the context of the geological time scale. Fossils indicated by hatched boxes, and refer to the oldest known representatives of those clades; apparent "tritomies" denote clades that had already differentiated into several subgroups, as evidenced by the fossil record; *mybp*, million years before present.



6

Tipulomorpha
Nymphomyiidae
Deuterophlebiidae
(Blephariceriinae)
Blephariceridae
(Edwardsininae)
Psychodomorpha
Ptychopteromorpha
* Culicomorpha
Axymyiomorpha
Bibionomorpha
"Cenozoic"
Cretaceous
Jurassic
Triassic
Permian
-65 mybp
-140 mybp
-210 mybp
-245 mybp
-290 mybp
Blephariceromorpha

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4. TAXONOMIC REVISION OF MOUNTAIN MIDGES (DIPTERA: DEUTEROPHLEBIIDAE).

4.1 Synopsis

Previously undescribed character systems are evaluated and incorporated in a redescription of the genus *Deuterophlebia* Edwards (Diptera: Deuterophlebiidae). The mountain midge fauna comprises 14 species, six of which are new. Four new species are Palaearctic, including *D. bicarinata* sp. nov. from southern Korea and *D. brachyrhina* sp. nov., *D. oporina* sp. nov., and *D. blepharis* sp. nov. from the Himalaya's of Sikkim and northeastern India (Assam). Two new Nearctic species are described. *Deuterophlebia personata* sp. nov. is widespread in mountains of western North America, with northern populations apparently parthenogenetic; *D. vernalis* sp. nov. occurs only in south-central Washington state. A lectotype is designated for *D. mirabilis* Edwards, and a lectotype and paralectotype are designated for *D. coloradensis* Pennak. Distributional data, and keys to larvae, pupae, and adults for all species are provided. Also presented is a general discussion of character variation in mountain midges, with particular reference to problematic Nearctic populations.

4.2 Introduction

Mountain midges (Diptera: Deuterophlebiidae) are an enigmatic family of nematocerous flies from western North America and eastern and central Asia. Their immature stages are aquatic and exhibit a variety of morphological specializations for life in swiftly flowing, often torrential, streams. Among these adaptations are eversible, crochet-tipped larval prolegs and a markedly streamlined pupa. Adults, which lack functional mouthparts and survive for only a few hours, exhibit equally aberrant features. Deuterophlebiids are of interest to both dipterist and aquatic entomologist, not only for their morphological and ecological specializations, but because the family is considered a primitive lineage of Diptera (Hennig 1973; McAlpine *et al.* 1981). Unfortunately, there is a significant lack of biological information on these unusual flies.

Recent investigations of deuterophlebiid systematics and ecology have led to the discovery of several new species, including two from western North America, and four from eastern and central Asia. This paper provides diagnoses, descriptions, distributional data, and bionomical and taxonomic notes about new and existing species, and a general discussion of structural variability in the family. Several new character systems are introduced, and serve as a basis for keys to the identification of adults, pupae and larvae of world species of *Deuterophlebia*.

4.3 Taxonomic History

The Deuterophlebiidae were originally described from two male imagos collected in the mountains of Kashmir, India (Edwards 1922). Shortly thereafter, Pulikovsky (1924) described *Deuterophlebia* larvae, pupae, and female imagos (dissected from pupae) from the Altai Mountains, Semipalatinsk (USSR). Because Pulikovsky lacked male imagos to compare with the description by Edwards, the Altai specimens were simply referred to as *Deuterophlebia* sp.. Pulikovsky provided a relatively detailed description of external and internal larval structure, and brief descriptions of two pupal morphotypes, one of which would be named almost 60 years later (Jedlicka and Halgos 1981).

Other central Asian *Deuterophlebia* records were given by Brodsky and Brodsky (1926) and Brodsky (1930), with the latter including a detailed treatment of larval structure. Brodsky (*loc cit.*) described two different female morphotypes (dissected from pupae), but referred to most central Asian material as *D. mirabilis*. Perhaps Brodsky's most valuable contribution to aquatic entomology and stream ecology was his major treatise "Mountain torrent of the Tien Shan" (Brodsky 1980). This English translation of "Gornyi potok Tian'-Shania" (Brodsky 1976) is a synthesis of geological, hydrological, physical, and biotic data, and represents perhaps the most detailed review of mountain streams of central Asia. Data about deuterophlebiids appear in several sections of the book, though most are based on earlier papers (especially Brodsky 1930).

Recent investigations of central Palaearctic deuterophlebiids have been conducted mostly by Czechoslovakian entomologists. These studies have led to discovery of a new species, *D. sajanica* Jedlicka and Halgos (Jedlicka and Halgos 1981), and general reviews of the distribution of Palaearctic species (Jedlicka 1980; Jedlicka and Halgos 1985).

After Edwards (1922), several years elapsed before the next published information about Himalayan deuterophlebiids. Singh (1961) reported on the collection of larvae of "an apparently undescribed species" from the north slope of the Pir Panjal Range and south slope of the Himalaya. Mani's treatises "Introduction to high altitude entomology" (1962) and "Ecology and biogeography of high altitude insects" (1968) also included reviews of Himalayan Deuterophlebiidae. Additional records of Himalayan mountain midges come from various abstracts (Kaul 1979; Kaul 1986) and papers (Dubey and Kaul 1971). Deuterophlebiids were also recorded from the Hindu Kush, northeast Afghanistan (Tokunaga 1966). However, the Himalayan fauna remains relatively unknown.

The history of deuterophlebiid research by Japanese dipterists dates back to late 1926, when larvae, pupae, and adult female *Deuterophlebia* were discovered near Kyoto (Kitakami 1929). Numerous additional specimens were recorded between 1926 and 1937, but lack of males prevented species identification (Kitakami 1938b). The first male pupa was collected (along with female pupa) on the island of Kyûshû (Kitakami 1938a); these specimens were supposedly "different than those...from Honsyû" (page 215, English translation). Differences were apparently insufficient to warrant recognition of separate species, since Kitakami described only one Japanese species, *D. nipponica* Kitakami, in "The Deuterophlebiidae of Japan" (Kitakami 1938b). This outstanding monograph did, however, contain a description of a second species, *D. tyosenensis* Kitakami, from Korea. Several years later, Kitakami (1954) reported collecting a large series of male imagos from the Hakugan River, North Korea. The paper presented mensural data for adult, including a table comparing *D. mirabilis*, Pulikovsky's *D.* sp., *D. nipponica*, and Hakugan specimens. Although Kitakami collected pupae and more than 140 adults, the identity of the Hakugan deuterophlebiids was not given, with all material simply listed as *Deuterophlebia* sp..

The first North American deuterophlebiid record was the 1921 collection of a small larva from the Yellowstone River, Wyoming (Muttkowski 1927). Subsequently, pupae were discovered in samples from the same area. Muttkowski gave a sketchy description and photograph of the immature larva, but little information about pupal structure.

A 1932 pupal sample from Jasper National Park, Alberta extended the known distribution of mountain midges considerably further north, and represented the first Canadian record (Shewell 1954). As discussed later, this material belongs to *D. inyoensis* Kennedy, described several years later from California's Sierra Nevada (Kennedy 1960).

During the 1940's, deuterophlebiids were collected in several parts of western North America, including Oregon, Colorado, and California. Since their discovery in 1942, mountain midges from Benton Co., Oregon have remained an enigma. This material has been variously identified as *D. coloradensis* Pennak (Pennak 1945; Stone 1949), *D. shasta* Wirth (Wirth 1951), or a new species (Kennedy 1960). Further details about this controversy are given later (see 4.5.3.14, *D. coloradensis*). *Deuterophlebia coloradensis* was described first from larvae and pupae collected from streams in northern Colorado (Pennak 1945). Descriptions of the male and female imago, and a taxonomic review of all described species, were part of a subsequent publication (Pennak 1951). Another new species, *D. shasta*, was discovered in 1948, near the headwaters of the South Fork Sacramento River, Siskiyou Co., California (Wirth 1951). Deuterophlebiids also were collected at several other California sites during the late 1940's (Kennedy 1954, 1958).

Harry D. Kennedy has played a major role in deuterophlebiid research in the Nearctic region. His interest in the group began in the early 1950's, while a graduate student at the University of Nevada - Reno. Kennedy's research focussed on the life history of a new species of mountain midge from Convict Creek, in California's eastern Sierra Nevada (Kennedy 1954). This study was the basis for his outstanding publication on *D. nielsoni* Kennedy (Kennedy 1958), and represents one of the most comprehensive investigations of a deuterophlebiid population, to date. Kennedy also collected aquatic insects from other streams in the Sierra Nevada, which led to the discovery of another new species of mountain midge, *D. inyoensis* (Kennedy 1960).

Subsequent to Kennedy's 1960 paper, most publications about Nearctic mountain midges have included either literature reviews (*e.g.*, Alexander 1963) or new collection records (*e.g.*, Arnaud 1974; Slack *et. al.* 1979; Babcock 1985; Turner *et. al.* 1986).

Special mention should be made of another New World collection record; namely, deuterophlebiids from central Chile (Stuardo 1953). Specimens, of unreported life stages, were allegedly collected by D.S. Bullock on October 10, 1951 and March 18,1952, near Angol, "in a southern tributary of the Rio Bio-Bio, the Rio Malleco and its branches" (Alexander 1963, pg. 74). Material was deposited in the Museo Nacional de Historia Natural, Santiago, but evidently has been lost (Kennedy 1985, *personal communication*). Additional specimens have not been collected, in spite of extensive searching by dipterists like C.L. Hogue, a well known blephariceríd specialist. Hogue has sampled many torrenticolous habitats in South America, including those of streams in the upper Rio Malleco drainage, near Angol; although blepharicerids are common to these areas, mountain midges have not been found (Hogue 1986, *personal communication*).

4.4 Materials and Methods

4.4.1 Materials. This study is based on examination of larvae, pupae, and/or adults of known species of *Deuterophlebia*. Specimens were borrowed from the following individuals and institutions; codens given here and throughout the text, indicate deposition of specimens:

AMNH	American Museum of Natural History, New York, USA (D. Grimaldi).

CNC	Biosystematics Research Centre, Ottawa, Canada (A. Borkent, D.M. Wood).
BMNH	British Museum (Natural History), London, England (B. Townsend).
CAS	California Academy of Sciences, San Francisco, USA (P.H. Arnaud, Jr.).
GWC	collection of author.
HDK	collection of H.D. Kennedy (material on indefinite loan to author).
LACM	Los Angeles County Museum of Natural History, Los Angeles, USA (C.L. Hogue).
OrSU	Oregon State University, Corvallis, USA (J.D. Lattin, N.H. Anderson).
PZW	collection of P. Zwick, Limnologische Flußstation des Max-Planck-Instituts für Limnologie.
ROM	Royal Ontario Museum, Toronto, Canada (G.B. Wiggins).
USNM	United States National Museum, Washington, USA (R.V. Peterson).
ZSM	Zoologische Staatssammlung, München, Federal Republic of Germany (W. Schacht).

Additional specimens (presently in the author's collection) were provided by L. Jedlicka, Comenius University, Bratislava, Czechoslovakia, S. Singh, St. John's College, Agra, India, M.J. Stansbury, Roseburg, Oregon, and D.A. Craig, D.C. Currie and E.R. Fuller, all of the University of Alberta.

4.4.2 Specimen Preparation. Material collected by the author was fixed in either 70% ethanol or Carnoy's solution. Most larval and pupal characters were evaluated at low magnification (<250X), from material in alcohol. Larvae cleared in cedarwood oil (as described in Courtney *in press*) and slide-mounted in Canada Balsam were preferable for discerning some features (*e.g.*, chaetotaxy). Examination of pupal microsculpture required slide-mounted specimens, with exuviae preferable, but pupae cleared in cedarwood oil, xylene or 10% potassium hydroxide (KOH) adequate. Pupae were mounted in Euparal or Canada Balsam.

Pin-mounted adults were prepared as follows: the head capsule and genitalia were removed, cleared (in lactic acid or KOH) and placed in glycerin; the remainder of the specimen was then critical point dried. Slide-mounted adults were dissected (head capsule, wings, legs from 1 side (left or right), and genitalia removed) and mounted in Euparal or Canada Balsam; most material was cleared in cedarwood oil or KOH prior to mounting. Evaluation of characters on air-dried, pinned adults proved difficult because of distortion and shrinkage, and necessitated rehydration in KOH, dissection and slide-mounting.

Specimens were examined and measured with a dissecting or compound microscope. Sample size for measurements varied with species and life stage, and is indicated prior to each data set. Measurements are expressed in millimeters, as a range of values followed by a mean and standard deviation in parentheses. Antennal article length ratios for adults are based on comparison to the shortest article, usually the pedicel, and represent the mean article length ratio of all measured individuals. Leg articles were measured along the dorsal margin; article percentages reflect mean values for the ratio of article length : total leg length.

Drawings were executed with the aid of a camera lucida or drawing tube, and photomicroscopy with a WILD Camera (MPS 51) and Microphotoautomat (MPS 45), using Kodak Plus-X 35mm film.

Larvae, pupae and adults of most species were also examined with a scanning electron microscope (SEM). Material for SEM examination was prepared by brief (<1 minute) sonication in ethanol (with 2-3 drops of concentrated ammonia added), followed by critical point drying, and gold-coating in a sputter coater. Prepared material was examined with either a Cambridge Stereoscan 100 or 250 SEM at 10-25kv. Observations were recorded on Kodak Plus-X or Ilford FP4 120mm roll film.

4.4.3 Terms for Structures. Terms for larval structures are from Courtney (*in press*, see chapter 2). Larval *antennal ratios* refer to the relative length of the proximal article : dorsal branch of distal article : ventral branch of distal article. The system of chaetotaxy provided by Courtney (*in press*) is used in the present work. Chaetotaxic features of importance for the larval key include the structure of sensilla *prl* and *sbt* (thoracic segments, Figs. 2, 3, 9, 10), *pm* (abdominal prolegs, Figs. 9, 10), *at* and *mt*, and sensilla group *ap* (latter three on abdominal segment VIII, Fig. 4).

Gender of instar IV larvae was determined by examining the posteroventral abdomen for genitalic primordia. Male larvae (Fig. 11) possess accessory gland primordia (*agp*) that are ovoid and relatively short, never extended anteriorly beyond abdominal segment VIII; males also have well-developed gonostylus primordia (*gsp*), which originate dorsolateral to anal papillae and terminate ventral to pupal sternite IX primordia (*sIX*). Female larvae (Fig. 12) possess accessory gland primordia that are elongate and extended anteriorly as far as abdominal segment V; basally, the primordia are contiguous with pupal sternite IX primordia.

Terms for pupae are based primarily on Kennedy (1958); however, terms for certain features are contradictory. Kennedy (1958) considered the pupal respiratory organs (spiracular gills) as part of the mesothorax, but later (Kennedy 1960, 1981) referred to them as prothoracic. The latter interpretation was also held by Pulikovsky (1924) and Wirth (1951), mostly because pupal gills develop within the larval prothorax. Hinton (1947) has shown that, although anterior larval spiracles are situated on the prothorax, they are, in fact, mesothoracic spiracles that migrate anteriorly during embryogenesis; similar development is reported for other Diptera (Campos-Ortega and Hartenstein 1985), and is probably typical of the order (Teskey 1981). Thus, the deuterophlebiid pupal gill is expected to develop near the vestigial anterior (mesothoracic) larval spiracle. This relationship is suggested further by continuity between the pupal gill and pharate adult mesothoracic spiracle, via a spiracular atrium or "felt" chamber (Hinton 1962).

Most taxonomically useful pupal characters pertain to the gills or macrosculpture. Gill characters include dimensions of the base, and patterns of filament association and bifurcation. The latter refers to whether or not the middle filament is most closely associated with the anterior or posterior filament, or if multiple filaments originate from a common base (*cf.* Figs. 27-30)[1]. Macrosculptural features include mesothoracic spines and tubercles ("conical protuberances" *sensu* Kennedy 1958, 1960), and thoracic and abdominal ridges. Structure of abdominal sutures (*i.e.*, whether or not they are traversed by secondary ridges) and mesothoracic rugosity are also examined. Pupal microsculpture may include dark, circular, *microtubercles* ("macro- [and] micro-ciliated granules" *sensu* Kennedy 1960) on abdominal and thoracic tergites (Figs. 41-46). Microtubercles may be glabrous or variously sculptured (*e.g.*, acinose), with this fine-scale microsculpture typically covering the cuticle between microtubercles. Microtrichia are often associated with microtubercles, and their position and length can be diagnostic for some species.

Terms for adult structures follow primarily McAlpine (1981), with Edwards (1922) and Kennedy (1958) valuable references pertaining to deuterophlebiids specifically. Determining homologies for cranial structures is difficult, because of the absence of functional mouthparts and distinctive sutures; therefore, most homologies are based on spatial relationships and landmark features (*e.g.*, tentorial pits). Edwards (1922), Kennedy (1958) and others have referred to the anterodorsal region of the cranium as the "clypeus". Because cranial sutures are not apparent, absolute clypeal boundaries can not be established; in spite of this, the term *clypeus* is retained in the present work, and refers to a region essentially delimited posteriorly by anterior tentorial pits and laterally by compound eyes. The absence of mouthparts makes establishing definitive homologies for the ventral cranium difficult. Therefore, the area surrounding the cibarium and more or less delimited posteriorly by the occipital foramen, laterally by the posterior tentorial pits, and anteriorly by the clypeus, is simply termed the *oral region* (Figs. 27, 28, 51-53); in many species, a *subgenal suture* (*sgs*) forms its lateral boundary. Structures near the cibarium (*cib*) include an anterior cluster of sensilla that may represent vestiges of maxillary palpi (indicated by asterisk in figures), and posteriorly, two clusters of sensilla (vestiges of labial palpi (*lmp*)), the salivary duct opening, and a *mental tooth* (*lmt*). That part of the oral region posterior and posterolateral to the mental tooth is called the *postgena* (*pg*). Although numerous cranial measurements and proportions (*e.g.*, distance between tentorial pits, antennal sockets) were analyzed, relatively few were of taxonomic value. Among the latter was length of the median clypeal lobe (Figs. 27, 28, *clm*) relative to the position of the anterior tentorial pits (*tpa*). The *clypeal incision* (*cli*), which delimits the median clypeal lobe of the adult male, is a reference point for both measurements.

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[1] When four filaments are present, this arrangement refers to the three longest filaments.

I deviate from most publications (Pulikovsky 1924; Kitakami 1938b; Pennak 1951; Wirth 1951; Kennedy 1958; and others) in my interpretation of the adult leg. I consider the femur (not the trochanter) to be the superficially "biarticled" leg segment, consisting of a short, narrow, *basal femur* and elongate, broad, *distal femur*. This decision is based partly on the arrangement of femoral muscles, which originate on the trochanter margin and insert on a darkly sclerotized apodeme at the proximal end of the basal femur. No other muscles traverse the basal femur, or flex the femur beyond this point. Furthermore, the trochanter-femur articulation is visible with the SEM, and demonstrates that the femur is the biarticled segment. In spite of continuity of these zones, the leg typically breaks between the basal and distal femur; this may have contributed to previous interpretations of structure. The adaptive significance of this arrangement becomes apparent by examining a pharate adult in the pupal case. The narrow and apparently flexible basal femur is situated in a zone where the posteriorly directed leg sheath bends anterolaterally. Because the basal femur must be flexible prior to eclosion, yet fully functional immediately as the adult reaches the water surface, it is expected that the region be ill-sclerotized and susceptible to breakage.

Male genitalia are relatively simple, and fusion of structures has obscured segmental boundaries. Tergites IX and X apparently are united into a large, plate-like, posteriorly bilobed (in most species), *dorsal plate* (Figs. 67, 73-80, *dp*). Anterolaterally, the dorsal plate is fused with the base of the gonocoxites (Fig. 67, *gc*), forming a *basal ring*.

4.4.4 Species Concept. Although a basic criterion for species recognition is reproductive isolation (Mayr 1969), lack of information about adult behaviour makes this criterion somewhat untenable. Indeed, the short life and limited vagility of deuterophlebiid imagos may effectively isolate most populations, even of a given species. I adopt essentially the evolutionary species concept of Simpson (1961) and Wiley (1978, 1981), and infer reproductive isolation by phenetic divergence, geographic distributions, and temporal patterns. If two or more forms overlap sympatrically and temporally, they are treated as separate species only if all forms retain their morphological distinctness. In most instances, allopatric populations also exist. When chorological data are unavailable or incomplete (*e.g.*, most Palaearctic species), decisions are based primarily on morphological criteria. Certain widespread taxa (*e.g.*, *D. coloradensis*) demonstrate marked regional variation in structure; however, intermediate populations suggest a continuum of variation not ascribable to hybridization. In these instances, my decisions about species recognition are, for the most part, rather conservative.

Decisions about species are somewhat biased by regional factors and by availability of material; *i.e.*, Nearctic species recognition depends to a great extent on immature stages, whereas the lack of comparable material for Palaearctic species demands a greater emphasis on the adult. Trends among Nearctic deuterophlebiids suggest that the diversity of the Palaearctic fauna will increase as more data become available about larvae and pupae.

4.4.5 Descriptive Format. Complete descriptions are given for most Nearctic species and all new Palaearctic species; otherwise, I refer to the original description. The latter is supplemented by personal observations, if the original reference did not include certain taxonomic information (*e.g.*, pupal microsculpture). Specimens listed immediately after type material are placed under "[Other] Material examined" or "Collection localities"; the former category is used when all specimens examined are to be listed, whereas the latter simply provides locality data. The latter category is used primarily for species that are widespread, and for which several thousand specimens were examined (including representatives from most localities and often from several different sample dates).

Label data, if recorded exactly as found on the label, are placed in quotation marks; supplemental information is given in square brackets. Abbreviations for labels include the following: *approx*, approximation; *C.G.*, Campground; *ca*, approximately; *Ck*, Creek; *confl*, confluence; *E*, East; *F.S.*, [United States] Forest Service; *Fk*, Fork; *Hwy*, Highway; *km*, kilometer(s); *M*, Middle; *mi*, mile(s); *N*, North; *NP*, National Park; *nr*, near; *R*, River; *Rd*, Road; *Res*, Reservoir; *S*, South; *trib*, tributary; *W*, West; *Xing*, Crossing / bridge

The treatments of taxa are arranged in a phyletic sequence (*i.e.*, plesiotypic species are listed prior to more apotypic species), as determined by a cladistic analysis of world species of *Deuterophlebia* (see chapter 6).

The descriptions of new species contained herein are the basis for descriptions in separate publications (*i.e.*, in refereed journals); under Article 8b of the International Code of Zoological Nomenclature, the author requests that neither this thesis, nor the descriptions contained herein, be considered as "published" (*sensu* ICZN).

4.5 CLASSIFICATION

4.5.1 Genus *Deuterophlebia* Edwards

Deuterophlebia Edwards 1922: 380; Pulikovsky 1924: 45; Brodsky 1930: 289; Lindner 1930: 33; Kitakami 1938b: 488; Pennak 1945: 1, 1951: 1; Wirth 1951: 49; Kennedy 1958: 206, 1960: 191; Jedlicka and Halgos 1981: 973.

Type species: *Deuterophlebia mirabilis* Edwards 1922 (by monotypy).

Diagnosis. Larva dorsoventrally flattened, eucephalous; antenna elongate, with bifurcate distal article; abdominal segments I-VII with paired, crochet-tipped, lateral prolegs; apneustic. Pupa oval, dorsoventrally compressed; male antennal sheath elongate, coiled around periphery of ventral abdomen; plastron-bearing spiracular gill on mesothorax, with short base and three or four filaments; abdominal segments III-V each with dark, ovoid, ventrolateral adhesive discs. Adult ♂ midge-like, hypognathous, with vestigial mouthparts; ocelli absent; tentorium well-developed; antenna markedly elongate, six-articled, with flagellomere 4 length *ca.* 90% total antennal length; thorax and wings large, with pronounced anal lobe, posteriorly fringed with long macrotrichia; primary veins reduced, but secondary venation distinct, numerous, fan-like; femur superficially bi-segmented; acropod without pulvilli, with one claw and large empodium set with capitate macrotrichia; abdomen without spiracles; terminalia simple, with tube-like aedeagus housed in an aedeagal sheath. Adult ♀ similar to male, but antenna short, length 0.5mm or less, acropod with two well-developed claws and setiform empodium; terminalia simple; genital fork small, internal; ovaries occupy most of abdomen and part of thorax; accessory glands large, elongate; spermathecae not apparent.

Description

Larval Instar IV (Fig. 1): Body 3-5mm in length, dorsoventrally flattened and slightly sclerotized, except head capsule. Head capsule eucephalous. Antenna elongate, bifurcate distally. Thoracic segments distinct; appendages absent. Abdomen eight-segmented; segments I-VII with paired, crochet-tipped, lateral prolegs. Anal papillae five in number. Apneustic. Body surface with dense microtrichia dorsally, glabrous ventrally.

Head slightly wider than long, dorsoventrally flattened. Dorsal cranium without ecdysial lines; dorsomedial margin darkly sclerotized, extended posteriorly into prothorax. Clypeus with anteromedial margin slightly produced; posterolateral margin forming tentorial phragma. Ventral cranium mostly membranous, but with darkly sclerotized, T-shaped, postgenal carina. Occipital condyles blunt, projected medially from, and delimiting juncture of, occipital and postgenal carina. Anterior tentorial pits distinct, at posterior terminus of tentorial phragma; tentorial arms unpigmented; posterior tentorial pits anteromedial to occipital condyles. Larval eye (stemmata) posterior to antennal base. Antenna biarticled; socket posterodorsally with small, dark, sclerotized band. Proximal article *ca.* four times longer than broad, dorsally with fine microtrichia. Distal article bifurcate; dorsal branch tapered toward apex, ventral branch cylindrical and blunt.

Labrum-epipharynx large, membranous, extended anteriorly from clypeus, curved ventrally, then posteriorly to cibarium. Epipharyngeal surface with two bands of enlarged spatulate macrotrichia; bands separated anteriorly, converging slightly posteriorly, terminated near U-shaped epipharyngeal bar. Lateral epipharyngeal surface with groups of elongate simple macrotrichia, narrowly united at base. Medial epipharyngeal surface set with solitary simple macrotrichia.

Mandible predominantly membranous. Base of mandible darkly sclerotized, ring-like, with thick ventral band, narrow lateral (aboral) bridge, and expanded, moderately sclerotized dorsal band. Basal mandibular hook blunt, distally directed, on adoral end of ventral ring. Prostheca dorsad of adoral end of ventral ring. Mandibular comb at apex of mandible with *ca.* 50 carinate teeth on ventral and labral margins. Subapical mandibular lobes membranous, on labral side of mandible, composed of one prominent lobe and one or two smaller lobes.

Maxilla with membranous cardo and three distinct lobes. Lacinia in form of a large, thick, mostly membranous, posterior lobe, supported by thin sclerotized rod; ventromedial margin with crescent-shaped band of macrotrichia; adoral margin with moderately dense elongate macrotrichia, and several thickened macrotrichia near labium. Stipes in form of a predominantly membranous, lateral (aboral) lobe, with small, lateral, crescent-shaped sclerite. Maxillary palp with small sclerite anteriorly, and 17 or 18 apical sensilla. Galea parallel and adpressed to anterior margin of lacinia, mostly membranous; ventral margin with band of long, thin, adorally directed macrotrichia; apex with small, elongate sclerite.

Labium with expanded, membranous postmentum. Prementum basally with numerous long, anteriorly extended macrotrichia; distal region bilobed, with long macrotrichia on lateral margins; medial margin of each lobe with four prominent conical sensilla. Premental sclerites paired, small, triangular, dorsolateral to labial sensilla. Hypopharynx in form of a small lobe between salivary duct opening and cibarium; hypopharyngeal suspensorium small, U-shaped.

Thorax dorsoventrally flattened, wider than head capsule; segments distinct, separated by lateral incisions, with round lateral margins.

Abdomen: Segments IV and V widest. Segments I-VII each with large, eversible, lateral prolegs (pseudopods), bearing rows of crochets distally. Proleg with 7-13 rows of crochets, with number variable between and within individuals; anteroventral and dorsal proleg surface with greatest and least number of crochet rows, respectively (due to partial rows ventrally). Crochets apically with five uniformly sized tines oriented parallel to proleg surface; crochets long, flat, and recurved medially, bifurcate basally. Prolegs with elongate macrotrichia along anterior and posterior margins. Anal segment (VIII) with two tapered, posteriorly directed appendages. Anal papillae of five thick, digitiform lobes on ventral side of anal segment, with four lobes ventral, and one dorsomedial, to anus.

Instar III: Similar to instar IV. Postgenal carina absent; ventromedial cranium with large, membranous, unpigmented postmentum; posterior tentorial pits on membranous cuticle near postmentum-gena boundary. Antennal socket without dark posterodorsal band; proximal article moderately sclerotized, with sparse microtrichia dorsally. Mandibular comb with *ca*. 40 teeth. Proleg with 5-8 rows of crochets.

Instar II: Similar to instar III. Body surface with sparse microtrichia dorsally. Proximal antennal article minute, unpigmented, glabrous. Mandibular comb with *ca*. 30 teeth. Thorax narrower than head capsule; prothorax indistinct, broadly fused with head capsule; mesothorax and metathorax separated by shallow lateral incisions. Proleg with three or four (depending on species) rows of crochets; number constant within individual.

Instar I: Similar to instar II. Body surface glabrous. Cranium dorsolaterally with distinct genae; medially membranous, except for elongate frontal sclerite. Frontal sclerite posteriorly extended into prothorax; anteriorly with tooth-like egg burster. Proximal antennal article absent. Epipharyngeal surface densely set with solitary simple macrotrichia; spatulate macrotrichia absent. Mandibular comb with *ca*. 20 glabrous teeth. Hypopharyngeal suspensorium anteriorly serrate. Prothorax indistinct. Proleg without macrotrichia on anterior and posterior margins; one row of crochets; crochets with 7-8 tines, oriented perpendicular to proleg surface; tines longest basally, progressively shorter distally.

Pupa (Figs. 13, 14): Body 2-4mm in length, broadly oval, dorsoventrally compressed. Dorsal surface anteriorly convex, posteriorly compressed; cuticle light brown (teneral specimens) to black. Ventral surface flattened; cuticle thin, pale. Head apparent only in ventral view, hidden beneath mesothorax in dorsal view; male antennal sheath (Fig 13, *an*) markedly elongate, coiled around periphery of ventral abdomen; female antennal sheath (Fig. 14, *an*) short, its apex extended posteriorly to base of wing sheath (*ws*).

Prothorax (Fig. 13, *pro*) indistinct, indicated at most by a faint groove anteroventral to gill base. Mesonotum (*mes*) large, broadly triangular in dorsal view, pointed anteriorly, slightly convex posteriorly, split medially by ecdysial line; posterolateral margin contiguous with abdominal segment I. Length of male mesonotum *ca*. 1/3 total body length; female mesonotum shorter, *ca*. 1/4 total body length. Gill situated on ventral margin of anterolateral mesothorax; composed of short base and three or four filaments. Metanotum (*met*) small, crescent-shaped, not extended laterally to margin of pupa. Wing sheath (*ws*) extended to posterior margin of abdominal segment IV. Male leg sheaths extended to anterior margin of abdominal segment VIII; mesothoracic leg sheath shortest, pro- and metathoracic leg sheaths subequal in length. Female prothoracic leg sheath extended to anterior margin of segment VIII, metathoracic leg sheath to segment IX, mesothoracic leg sheath to intermediate position.

Abdominal segments I - VII narrow medially, expanded laterally. Segments I and II with lateral margins anteriorly projected and bearing several darkly sclerotized, thorn-like spines. Segments V - VII posterolaterally produced. Segments VI and VII posterolaterally with small thorn-like spines. Segments VIII and IX laterally surrounded by posterior margin of segment VII. Segments III-V each with dark, ovoid, adhesive disc (*ad*) on ventrolateral margins.

Adult ♂: Delicate, midge-like fly; body length 2-4mm. Head and thorax dark brown to black, abdomen light brown. Hypognathous; mouthparts vestigial. Antenna markedly elongate, six-articled. Thorax and wings enlarged, wings silvery-blue. Legs similar, long, thin. Abdomen broad basally, tapered distally. Body surface generally set with microtrichia.

Head (Figs. 31, 49-53) small, transverse, *ca*. 1.5 times broader than long, hidden in dorsal view beneath projecting mesonotum; cranium dorsoventrally flattened anteriorly, thicker posteriorly. Cranium dorsally without apparent sutures. Compound eye small, subspherical, dichoptic, composed of *ca*. 150 uniformly sized facets; in most species, eyes without microtrichia. Distance between eyes *ca*. half the maximum width of head. Ocelli absent. Anterior (*tpa*) and posterior (*tpp*) tentorial pits distinct. Cranium ventromedially concave; mouthparts vestigial (Figs. 31, 55-57). Cibarium (*cib*) posteroventral to median clypeal lobe, oval in shape. Oral region anteriorly with cluster of six peg-like sensilla, arranged in two groups of three (maxillary palps?). Labial palps (*lmp*) paired, peg-like, situated immediately posterolateral to cibarium. Salivary duct opening posterior to labial palps, hidden in ventral view by small, blunt mental tooth (*lmt*). Postocciput darkly sclerotized, ventrolaterally expanded into large occipital condyles (*oco*); postoccipital suture distinct. Occipital foramen (*ocf*) large, width *ca*. 70% maximum width of head.

Antenna to 16mm maximum length. Antennal socket large, subtriangular, broad laterally and tapered medially (Fig. 31, *ans*); width *ca*. 25% maximum width of head. Scape (Fig. 33, *sc*) subcylindrical, broader than pedicel (*ped*), densely set with microtrichia on dorsal surface; pedicel cup-shaped, about as long as broad, dorsally with fine microtrichia. Flagellomeres 1-3 (f1-3) cylindrical, sparsely covered with microtrichia (Figs. 33, 59-61); f1 longer than f2 or f3. Flagellomere 4 markedly elongate, length *ca*. 90% of total antennal length; f4 base slightly broader than f3, tapered gradually to near apex, with apex expanded; dorsal surface darkly sclerotized, basally with sparse microtrichia; ventral surface slightly sclerotized, with small, curved sensilla; sensilla relatively dense basally, absent distally except for *ca*. 20 on apex. Intersegmental membrane broad, unpigmented.

Prothorax reduced. Cervical sclerites two in number, thin, elongate, laterally situated, articulated to occipital condyles. Antepronotum and postpronotum slender, rod-like, each with small, dorsolaterally produced lobe. Prosternum forms anterior-, medial-, and posterior margin of forecoxa; precoxal and postcoxal bridge apparent.

Mesothorax, particularly mesonotum, markedly enlarged. Prescutum broad, anteriorly convex, extended over head. Prescutal suture distinct laterally, contiguous with parapsidal sutures medially; prescutum and scutum contiguous medially. Transverse sutures absent. Median scutal suture distinct. Scutum laterally convex, medially flattened; posterior margin more or less straight. Postalar ridge distinct. Scutellum short, broadly rectangular; anteromedial margin slightly convex; supra-alar depression distinct; posterior scutellar margin straight, except for small, semicircular, posteriorly directed projection laterally. Postnotum large, anteriorly exposed, broader than scutellum, moderately convex; posteriorly constricted, extended to abdominal segment III; posteromedial margin notched. Mesopleuron obliquely elongate. Episternum large, broadly elongate; anapleural suture faint; anepisternal membrane broad, set with 10-20 small setiform sensilla, posteriorly with small cleft; anepisternum elongate posterodorsally, its apex truncate; katepisternum broadly ovoid, extended posteriorly beyond hind margin of midcoxa. Subalare broadly elliptical, with *ca.* 15 prominent setiform sensilla. Anepimeron distinctly divided; dorsal region slender, projected posteriorly toward scutellum; anterior region enlarged, bulbous, with several setiform sensilla; katepimeron small, rectangular. Meron subquadrate, dorsally contiguous with laterotergite. Mesosternum exposed, enclosing midcoxal base anteriorly, medially, and posteriorly.

Metanotum medially bisected, posteriorly extended to abdominal segment III. Metepisternum small, triangular, enclosing spiracle. Metepimeron thin, hidden by meron in lateral view. Metasternum exposed anterior and medial to hindcoxal base.

Wing 3-6mm in length, with large anal lobe; posterior margin with fringe of long macrotrichia basally, becoming shorter and less numerous distally; wing membrane set with microtrichia. Veins reduced; C terminated near wing tip; Sc terminated in R_1 slightly beyond middle of wing; R_1 parallel to Sc basally, curved slightly toward wing margin, terminated in C; R_{2+3} faint basally, gradually curved anteriorly, terminated in C; R_{4+5} evanescent basally, extended nearly to wing margin; M_1 evanescent basally, parallel to R_{4+5}, terminated before wing margin; M_2, CuA_1 and CuA_2 short, extended toward, but terminated before, wing margin; A_1 variably distinct, terminated near base of anal lobe. Secondary venation fan-like, with numerous longitudinal lines and three concentric lines.

Halter stem slender, basally with 2-3 setiform sensilla; halter knob globose; entire surface set with microtrichia.

Foreleg: coxa cylindrical, trochanter barrel-shaped, both with distinct patches of campaniform sensilla. Femur superficially bi-segmented; basal femur short, darkly-pigmented, thinner than trochanter, with several campaniform sensilla ventrally; distal femur basally pale, lightly sclerotized; femur dorsally with several setiform sensilla. Tibia proximally thin, distally expanded, with setiform sensilla mostly on dorsal surface; tibia distally with capitate or simple macrotrichia (Figs. 60, 63, 64). Tarsus five-segmented; ventral surface with capitate or simple macrotrichia, and several chaetiform sensilla; tarsomere five dorsally with two prominent setiform sensilla. Acropod (Fig. 65) with one claw; empodium (*emp*) conspicuous, circular, flattened, densely set with capitate macrotrichia; pulvilli absent. Midleg similar to foreleg, but slightly shorter, more robust. Hindleg similar to foreleg, but with relatively elongate femur.

Abdomen without spiracles. Segments I-III short, IV-VII relatively long; tergites moderately sclerotized, sternites predominantly membranous. Segments VI and VII posteriorly with row of chaetiform sensilla extended from dorsomedial to lateral margin; row terminated at small, papilliform protuberance with several chaetiform sensilla. Tergite VIII in form of a sclerotized partial ring surrounded by membranous cuticle, usually with two setiform sensilla; sternite VIII broadly triangular.

Terminalia simple (Fig. 67). Tergite IX and sternite IX anterolaterally fused, forming a basal ring. Posterior margin of dorsal plate variously shaped (Figs. 67, 73-80), set with setiform and/or chaetiform sensilla. Gonocoxite slightly tapered distally, membranous medially. Gonostylus simple; medial and apical margin with short, recurved spines. Aedeagus (Figs. 68, 69) tube-like, slightly tapered posteriorly, usually curved dorsally at apex; aedeagal sheath tube-like, originating at inner base of gonocoxites, typically with several small sensilla dorsally.

Adult ♀: Similar to male. Compound eye with *ca*. 100 facets. Antennal socket small, subcircular (Fig. 32, *ans*). Antenna short, length 0.5mm or less (Fig. 34); scape (*sc*) cylindrical, width subequal to pedicel (*ped*). Flagellomere 1 longer than f2, f3, or f4; f1-4 set with microtrichia, apically with digitiform sensilla on anteroventral margin; f4 bearing several setiform sensilla.

Relative to male, thorax and wing smaller; anal lobe of wing less developed.

Legs similar; femur more robust than in male; tibia uniformly thick, without capitate macrotrichia. Tarsus without macrotrichia; length of t1 variable; t2, t3, and t4 subequal in length and each less than half the length of t5. Acropod (Fig. 66) with two well-developed claws; empodium (*emp*) setiform.

Abdomen broad, tapered only at terminalia. Terminalia simple: Sternite VIII (hypogynium) elongate, with longitudinal groove medially and two blunt lobes apically. Genital fork (sternite IX, Figs. 35-37, *gf*) small, internal, plate-like, typically situated on dorsal side of abdomen; genital fork triangular, anteriorly blunt or tapered ("notum" *sensu* Saether 1977), posteriorly broad and divergent, forming two expanded, pigmented, dorsolateral lobes ("rami" *sensu* Saether 1977) and two unpigmented lateral and ventral lobes ("coxosternapodeme IX" and "labia", respectively, *sensu* Saether 1977). Tergite X medially bisected, apically bilobed; each lobe dorsomedially with several peg-like sensilla, and apically with a short, superficially biarticled cercus (Fig. 35, 70-72, *cer*). Ovaries large, occupying most of abdomen and posterior part of thorax. Accessory glands (base shown on Fig. 35, *ag*) large, elongate, extended anteriorly to beyond genital fork, abruptly curved ventrad, then anteriorly to posterior margin of thorax. Spermathecae not apparent.

4.5.2 Keys to Species of *Deuterophlebia*

4.5.2.1 Key to instar IV larvae[1]

1 Sensilla *prl* (Fig. 3), *at* and *mt* (Fig. 4a) simple; dorsal cranium predominantly dark 2

Sensilla *prl* (Fig. 2), *at* and *mt* (Fig. 4b) branched; dorsal cranium variously colored 4

2(1) Distal antennal article with dorsal branch markedly elongate, its length *ca.* five times the length of proximal antennal article (Fig. 10); pit-like sensillum near apex of ventral branch; northwest Himalaya .... *D.* sp. B

Distal antennal article with dorsal branch length *ca.* 2-3 times the length of proximal antennal article (Figs. 1-3, 5-9); pit-like sensillum near base of ventral branch; Nearctic 3

3(2) Distal antennal article with vestiture of digitiform microtrichia (Fig. 39); antennal ratio *ca.* 1:3:1; sensilla group *ap* with two clusters of several digitiform sensilla (Fig. 4b); dorsal cranium entirely dark (Fig. 5) .... *inyoensis*

Distal antennal article without microtrichia (Fig. 38); antennal ratio *ca.* 5:10:3; sensilla group *ap* with only two digitiform sensilla (Fig. 4a); dorsal cranium either anteriorly dark, in region delimited posteriorly by antennal bases (and including clypeal lobe), or dorsal cranium entirely dark, but noticeably darker anterior to level of antennal base (Fig. 3) .... *shasta*

4(1) Meso- and metathorax, and abdominal segments I-VII with prominent dorsal protuberances lateral to midline; abdomen with smaller protuberances at base of each proleg (Fig. 8); Coast Range, Oregon .... *coloradensis* (in part)

Thorax and abdominal segments without dorsal protuberances 5

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[1] Larvae unknown for *D. mirabilis* (*i.e.*, none definitively associated with adults), *D. brachyrhina*, *D. oporina*, and *D. blepharis*; because only one damaged larva of *D. nipponica*, and none of *D. tyosenensis*, were examined, these species are excluded from the key.

5(4) Clypeal lobe pale; dorsal cranium with or without distinct color pattern (Figs. 6-8). .... *coloradensis* (in part), *nielsoni*

Clypeal lobe dark; dorsal cranium with distinct color pattern (Figs. 1, 2, 9) 6

6(5) Sensilla group *ap* with only two digitiform sensilla (Fig. 4b); sensilla *sbt* (meso- and metathorax) lanciform (as in Fig. 10); Nearctic 7

Sensilla group *ap* with two clusters of several digitiform sensilla (as in Fig. 4a); sensilla *sbt* (meso- and metathorax) setiform (Figs. 9); Palaearctic.............. 8

7(6) Dorsal cranium mostly pale, with dark, medial, triangular patch, the base of which is delimited anteriorly by the clypeus and mandibles, and apex of which is extended posteriorly to near anterior margin of prothorax (Fig. 2); south-central Washington .... *vernalis*

Dorsal cranium anteriorly with dark, rectangular patch across clypeal lobe; dorsal cranium posteriorly pale in some populations, but typically with dark "mask-like" patch extended between, and covering, stemmata (Fig. 1); widespread Nearctic .... *personata*

8(6) Sensilla *pm* branched (Fig. 9); dorsal cranium with distinct color pattern, with clypeal lobe dark at base, light distally (Fig. 9) .... *bicarinata*

Sensilla *pm* setiform (as in Fig. 10); dorsal cranium predominantly dark, including clypeal lobe .... *sajanica*

4.5.2.2 Key to pupae[1]

1 Anterolateral margin of mesothorax with spine-like processes (Figs. 13, 14, 16, 19, 22-24) 2

Anterolateral margin of mesothorax without spine-like processes, though darkly-sclerotized tubercle on some specimens (Figs. 15, 17, 18, 20, 21, 26) 8

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[1] Pupae unknown for *D. mirabilis* (*i.e.*, none definitively associated with adults), *D. brachyrhina*, D. *oporina*, and *D. blepharis*.

2(1) Mesothoracic gill with four filaments, with posterior-most filament in the form of a thick, posteriorly directed lobe (Fig. 27); Palaearctic.............................. 3

Mesothoracic gill with three filaments (Figs. 28-30); Nearctic 6

3(2) Mesothorax with two, stout spines on each anterolateral margin (Figs. 24, 25); abdominal microtubercles absent or, if present, uniformly distributed over tergite; posterior-most gill filament short, its length subequal to its width....... 4

Mesothorax with a single, finely tapered spine on each anterolateral margin (Figs. 22, 23); abdominal tergites set with microtrichia, but microtubercles sparse, and restricted mostly to cuticle near sutures; posterior-most gill filament long, its length approximately twice as long as wide (Fig. 27).............................. 5

4(3) Abdominal microtubercles absent; mesonotum more or less glabrous (except for a pair of transverse bands), without raised, sclerotized dots; small (length *ca.* 2mm); Korea .... *tyosenensis*

Abdominal microtubercles abundant, with apical microtrichia; mesonotum markedly rugose and with one pair of small, raised, sclerotized dots anterodorsally (Fig. 25); large (length greater than 3mm); Nepal........ *D.* sp. C

5(3) Abdominal segments I and II each with a transverse, raised, darkly-scleritized band on either side of the dorsal midline (Fig. 22); Korea............... *bicarinata*

Abdominal segments without darkly-scleritized bands on either side of the dorsal midline (Fig. 23), central Asia .... *sajanica*

6(2) Mesothoracic spine thick, short, its apex rarely extended anteriorly beyond level of gill base (Fig. 19); Coast Range, Oregon.....................*coloradensis* (in part)

Mesothoracic spine narrow, elongate, its apex extended anteriorly to near outer margin of gill filament (Figs. 13, 14, 16)... 7

7(6) Abdominal tergites without microtubercles, but with clusters of microtrichia (Fig. 40); abdominal sutures with secondary ridges; mesothoracic spine finely tapered, its apex extended beyond outer margin of gill (Fig. 16) .... *shasta*

Abdominal tergites with distinct microtubercles and associated basal microtrichia (Fig. 43); abdominal sutures simple, without secondary ridges (as in Fig. 42); mesothoracic spine relatively robust, its apex rarely extended beyond outer margin of gill (Figs. 13, 14).. *personata*

8(1) Abdominal tergites I-VII each with a prominent tubercle (Fig. 20) or transverse, raised, darkly-scleritized band on either side of midline (Fig. 26)................ 9

Abdominal tergites without prominent tubercles or darkly-scleritized bands on either side of midline (Figs. 15, 17, 18, 21) 10

9(8) Abdominal tergites I-VII each with a prominent tubercle on either side of midline (Fig. 20); abdominal sutures simple, without secondary ridges, and abdominal microtubercles present, with basal microtrichia (Fig. 42); Coast Range, Oregon .... *coloradensis* (in part)

Abdominal tergites I-VII each with a transverse, raised, darkly-scleritized band on either side of midline, and an irregularly shaped, raised, darkly-scleritized dot farther toward lateral margin (Fig. 26); abdominal sutures with secondary ridges (as in Fig. 40); abdominal microtubercles sparse, restricted mostly to cuticle near sutures; Japan .... *nipponica*

10(8) Gill base length subequal to width, situated on ventrolateral protuberance on mesothorax (Figs. 15, 28); mesonotum markedly rugose; abdominal microtubercles densely covered with microtrichia (Fig. 41)............ *inyoensis*

Gill base broader than long, not situated on ventrolateral protuberance (Figs. 17, 18, 21); mesonotum slightly rugose, usually with only simple ridges; abdominal microtubercles with basal microtrichia (Figs. 42, 44, 45)...........11

11(10) Middle gill filament most closely associated with anterior filament, typically arising from a common base (Figs. 17, 29); abdominal microtubercles with irregular sculpturing (Fig. 44); Sierra Nevada, California........................... *nielsoni*

Middle gill filament most closely associated with posterior filament, typically arising from a common base (Figs. 18, 21, 30); abdominal microtubercles smooth or acinose (Figs. 42, 45) 12

12(11) Anal projection on posteromedial margin of segment IX (Fig. 48)[1]; abdominal microtubercles acinose, with associated microtrichia short, not extended radially to adjacent microtubercles (Fig. 45); south-central Washington .... *vernalis*

Anal projection absent (Fig. 47); abdominal microtubercles smooth, with associated microtrichia long, typically extended radially to adjacent microtubercles (Fig. 42); widespread .... *coloradensis* (in part)

4.5.2.3 Key to adult males[2]

1 Antennal length 7mm or less, with flagellomere 4 length less than 90 times longer than pedicel; Assam 2

Antennal length 8mm or more, with flagellomere 4 at least 110 times longer than pedicel 3

2(1) Tibia and tarsus without capitate macrotrichia (Fig. 63); posterior margin of dorsal plate with deep medial excision (Fig. 73); median clypeal lobe indistinct (Fig. 49); postgena and oral region glabrous (as in Fig. 57); flagellomeres 1-3 with *ca.* 5, 20, and 30 digitiform sensilla, respectively, on anteroventral margin (Fig. 59); hind tarsomere 1 thickened, its width greater than width of basal tibia (Fig. 62); active in Spring .... *brachyrhina*

Tibia and tarsus with capitate macrotrichia (as in Fig. 58); posterior margin of dorsal plate truncate (Fig. 74); median clypeal lobe truncate (Figs. 50, 55); postgena and oral region set with microtrichia (Fig. 55); flagellomeres 1-3 each with less than 10 digitiform sensilla on anteroventral margin; hind tarsomere 1 not thickened, its width subequal to width of tarsomeres 2-5 and less than width of basal tibia; active in Autumn..*oporina*

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[1] Anal projection most noticeable on male pupae.

[2] Males unknown for *D. tyosenensis*. Adult males of *D. nipponica* were not examined; thus, its placement in the key is tentative (and based primarily on Kitakami (1938) and female characteristics).

3(1) Postgena set with microtrichia, and subgenal suture indistinct (Fig. 56)............4

Postgena glabrous, and subgenal suture usually distinct (Figs. 31, 57).............6

4(3) Median clypeal lobe apically truncate and elongate, its length exceeding the distance between the clypeal incision and anterior tentorial pits (as in Fig. 51; see also Fig. 56); flagellomeres 1-3 with digitiform sensilla not borne on anteroventral prominence (Fig. 60); foretibia distally without macrotrichia on dorsal margin (Fig. 64); length of gonostylus subequal to or less than length of aedeagal sheath; posterior margin of dorsal plate truncate or shallowly emarginate (Fig. 75); Nearctic.. *inyoensis*

Median clypeal lobe apically rounded and short, its length less than the distance between the clypeal incision and anterior tentorial pits (as in Figs. 31, 52, 53); flagellomeres 1-3 each with digitiform sensilla borne on anteroventral prominence (as in Fig. 62); foretibia distally with capitate macrotrichia on dorsal margin (as in Fig. 58); length of gonostylus greater than length of aedeagal sheath; posterior margin of dorsal plate; Himalaya or central Asia................5

5(4) Compound eyes with microtrichia between facets (Fig. 54).................*blepharis*

Compound eyes glabrous (as in Fig. 53).. *mirabilis*

6(3) Aedeagus internally with numerous, subparallel ridges on ventral margin (Fig. 68); median clypeal lobe elongate, its length subequal to the distance between clypeal incision and anterior tentorial pits (Fig. 51); length of gonostylus subequal to or less than length of aedeagal sheath median .... *shasta*

Aedeagus internally without ridges, ventral margin smooth (as in Fig. 69); median clypeal lobe short, its length less than the distance between clypeal incision and anterior tentorial pits (Figs. 31, 52, 53; as in Fig. 49); length of gonostylus greater than length of aedeagal sheath...7

7(6) Antennal f1 bulbous distally and with *ca.* 25 digitiform sensilla on anteroventral margin; median clypeal lobe indistinct (as in Fig. 49)......... *bicarinata, sajanica*

Antennal f1 not bulbous distally and with no more than 10 digitiform sensilla on anteroventral margin; median clypeal lobe short, convex (Figs. 31, 52, 53).... 8

8(7) Posterior margin of dorsal plate deeply emarginate (Fig. 77)........................ 9

Posterior margin of dorsal plate shallowly emarginate or medially notched (Figs. 78-80)... 10

9(8) Dorsal plate with lateral margins slightly concave, and anterolateral margins narrowly fused to gonocoxites (Fig. 77); south-central Washington..... *vernalis*

Dorsal plate with lateral margins divergent, and anterolateral margins broadly fused to gonocoxites (*cf.* Kitakami 1938b, Fig. 7); Japan....................... *nipponica*

10(8) Dorsal plate with lateral margins more or less parallel-sided, and posterior margin shallowly emarginate and medially notched (Fig. 78) .... *personata*

Dorsal plate shape variable, but typically without above combination of features (Figs. 79, 80) ....*coloradensis, nielsoni*

4.5.2.4 Key to adult females[1]

1 Postgena and oral region set with microtrichia (as in Figs. 55, 56); antennal f1 longer than scape.. 2

Postgena and oral region glabrous (Fig. 32; as in Fig. 57); antennal f1 shorter than scape (Fig. 34).. 5

2(1) Hind tarsomere 1 long, length of t1/t5 greater than 0.6; anterior bridge of genital fork extended posteriorly to less than half the distance to accessory gland opening (Fig. 37); Nearctic... *inyoensis*

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[1] Females unknown for *D. brachyrhina* and *D. tyosenensis*. Examined females included only two each of *D. bicarinata* and *D. sajanica*, and a single, damaged *D. nipponica*, all of which had been dissected from pupae; thus, the placement of these three species in the key is very tentative.

Hind tarsomere 1 short, length of t1/t5 less than 0.6; anterior bridge of genital fork extended posteriorly to more than half the distance to accessory gland opening (as in Fig. 36); Palaearctic 3

3(2) Compound eyes with microtrichia between facets (as in Fig. 54)........... *blepharis*

Compound eyes glabrous (as in Fig. 53).. 4

4(3) Dorsal margin of scape with two prominent setiform sensilla; cercus markedly elongate, with length of basal article at least twice the length of distal article; anterior bridge of genital fork extended posteriorly to less than half the distance to accessory gland opening (as in Fig. 37); small (wing length 3-4mm)........... .... *oporina*

Dorsal margin of scape without setiform sensilla; cercus stout, short, with length of basal article subequal to length of distal article; anterior bridge of genital fork extended posteriorly to more than half the distance to accessory gland opening; large (wing length >5mm) .... *mirabilis*

5(1) Hind tarsomere 1 long, length of t1/t5 greater than 0.6; south-central Washington.. .... *vernalis*

Hind tarsomere 1 short, length of t1/t5 less than 0.6 6

6(5) Cercus with length of basal article less than length of distal article (Fig. 70)......... .... *bicarinata, shasta*

Cercus with length of basal article subequal to or greater than length of distal article (Figs. 71, 72) 7

7(6) Cercus with basal and distal articles indistinctly fused to each other, with the point of fusion marked only by an indistinct, ventrolateral notch (Fig. 72); antennal f4 long, its length greater than length of f3 .... *sajanica, personata*

Cercus with basal and distal articles distinguishable by constriction on all but medial margin (Fig. 71); antennal f4 short, its subequal to length of f3 ....*nipponica, coloradensis, nielsoni*

4.5.3 Classification of Species

4.5.3.1 *Deuterophlebia brachyrhina* sp. nov.

(Figs. 49, 59, 62, 63, 73, 81)

Diagnosis. Male similar to *D. oporina*, but readily distinguished by the following features: tibia and tarsus without capitate macrotrichia; median clypeal lobe indistinct; hind tarsomere 1 thickened, its width greater than that of tibia base; posterior margin of dorsal plate with deep median notch.

Description

Larva: Unknown.

Pupa: Unknown.

Adult ♂: Median clypeal lobe indistinct (Fig. 49); clypeus medially with *ca.* 25 setiform sensilla; lateral lobes slightly developed, densely set with microtrichia. Anterior tentorial pits *ca.* 60µm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture distinct, extended from lateral clypeal lobe to posterior tentorial pit; postgena and oral region glabrous, except for few microtrichia and setiform sensilla near anterior clypeal margin (as in Fig. 57); mental tooth acute. Antennal f1, f2 and f3 slightly bulbous distally and with a cluster of *ca.* 5, 20, and 30 digitiform sensilla, respectively, on anteroventral margin (Fig. 59). Coxa, trochanter and femur without macrotrichia, but with dense microtrichia. Forecoxa markedly shortened, subspherical in shape. Fore-, mid- and hindtibia with simple macrotrichia, without capitate macrotrichia (Fig. 63). Hind tibia posteriorly glabrous, with patch of elongate, apparently stiffened macrotrichia near tibiotarsal joint (Fig. 62). Hind t1 thickened, its width greater than that of tibial base; t1 posteriorly glabrous. All tarsi without capitate macrotrichia.

Terminalia: Dorsal plate (Fig. 73) posteriorly with deep median notch; posterior margin with setiform and chaetiform sensilla; posterolateral angle acute; lateral margins parallel-sided. Gonostylus length subequal to length of dorsal plate, greater than length of aedeagal sheath. Aedeagus internally smooth.

Measurements (N=6): Total body length 1.9-2.2mm (2.04±0.09). Antennal length 5.6-6.9mm (6.13±0.02); article length ratio 4:1:2.5:2:2:91. Wing length 4.0-4.6mm (4.23±0.21), width 2.0-2.3mm (2.12±0.13). Leg article percentages: foreleg - 4:4:24:39:16:4:4:3:3; midleg - 8:5:27:33:12:4:4:3:3; hindleg - 8:5:33:33:12:3:3:2:3.

Adult ♀: Unknown.

Holotype ♂: "Nyukmadong, NEFA, Kameng, Fr. Div. Assam, INDIA, 7300' [ca. 27°26'N 92°08'E], 23.IV.1961, F. Schmid"; specimen on slide (in Euparal); [CNC].

Paratypes: Same data as holotype, 19♂ [7 on slides, 12 pinned]; 18.IV.1961, 7♂ [pinned]; "Kelong, NEFA., Kameng Fr. Div., Assam, INDIA, 6000', 26.IX.61, F. Schmid", 1♂ [on slide]; paratypes deposited in CNC, BMNH, USNM and GWC

Derivation of specific epithet: From the Greek for "short snout", in reference to the indistinct median clypeal lobe.

Distribution: Known only from the Himalaya of northern Assam (Fig. 81).

Bionomics: Type material apparently was collected from swarms over streams (Schmid 1988, *personal communication*). Collection records suggest that *D. brachyrhina* is active during the Spring, and is temporally isolated from other species (*cf. D. oporina* and *D. mirabilis*). However, the 26.IX.61 collection of a single specimen from Kelong seems to refute this hypothesis, and suggest further that *D. brachyrhina* may have more than one generation. Alternatively, the Kelong male may be labelled incorrectly; *i.e.*, the collection date may be 26.IV.61, rather than 26.IX.61.

4.5.3.2 *Deuterophlebia oporina* sp. nov.

(Figs. 50, 55, 74, 81)

Diagnosis. Male similar to *D. brachyrhina* but identified by the following features: tibia and tarsus with capitate macrotrichia; median clypeal lobe with truncate apex; mental tooth bilobed; posterior margin of dorsal plate truncate. Female distinguished from other species by two prominent setiform sensilla on the dorsal margin of the scape, and by the markedly elongate cercus (with most of its length consisting of the basal article).

Description

Larva: Unknown.

Pupa: Unknown.

Adult ♂: Median clypeal lobe pronounced, subquadrate, with truncate apex (Fig. 50); clypeus medially with *ca.* 15 setiform sensilla; lateral lobes slightly developed, with sparse microtrichia. Anterior tentorial pits *ca.* 40µm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture indistinct; postgena and oral region with microtrichia; mental tooth bilobed (Fig. 55). Each of antennal f1, f2 and f3 distally with *ca.* six digitiform sensilla, borne on anteroventral tubercle. Coxa, trochanter and femur without macrotrichia; fore and middle tibia distally with abundant capitate macrotrichia, especially on ventral margin (as in Fig. 58). Hind tibia with capitate macrotrichia on ventral margin. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate (Fig. 74) subquadrate; posterior margin truncate, with setiform sensilla. Gonostylus length subequal to length of both dorsal plate and aedeagal sheath. Aedeagus internally smooth.

Measurements (N=7): Total body length 1.9-2.2mm (2.09±0.11). Antennal length 5.5-6.0mm (5.74±0.25); article length ratio 2.5:1:2.5:1.5:1.5:87. Wing length 3.7-4.0mm

(3.85±0.11), width 1.6-1.9mm (1.77±0.10). Leg article percentages: foreleg - 7:4:23:36:16:5:4:3:3; midleg - 8:4:26:30:17:5:4:3:3; hindleg - 8:4:31:35:9:4:4:3:3

Adult ♀: Similar to male. Median clypeal lobe pronounced, *ca*. 45µm long, with *ca*. ten setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca*. 12µm posterior to clypeal incision. Antenna with dorsal margin of scape with two prominent setiform sensilla; pedicel with *ca*. four setiform sensilla; f1-3 distally with two, three, and four digitiform sensilla, respectively; f4 with five setiform sensilla and three digitiform sensilla.

Terminalia: Anterior bridge of genital fork posteriorly convex and extended less than half the distance to accessory gland opening (as in Fig. 37). Cercus with length of basal article at least twice length of distal article; articles distinguishable by constriction on all but medial margin (as in Fig. 71).

Measurements (N=2): Total body length 1.4-2.1mm. Antennal length 0.33mm; article length ratio 2.5:1:3.5:1.5:1.5:1. Wing length 3.3-3.4mm, width 1.3-1.4mm. Leg article percentages: foreleg - 7:4:23:41:6:4:4:4:9; midleg - 8:4:23:39:6:4:4:4:8; hindleg - 9:4:25:38:4:4:4:4:10. Length of t1/t5: foreleg -.65-.70; midleg -.60-.72; hindleg -.45.

Holotype ♂: "Phutang, NEFA., Kameng Fr. Div., Assam, INDIA, 7300' [ca. 27°14'N 92°14'E], 1-2.X.61, F. Schmid"; specimen on slide (in Euparal); [CNC].

Allotype ♀: Same data as holotype; specimen on slide (in Euparal); [CNC].

Paratypes: Same data as holotype, 54♂ [6 on slides, 48 pinned] 2♀ [1 on slide, 1 pinned]; "Ramtang, Sikkim, 5780', 13.X.59, F.Schmid", 9♂ [1 on slide, 8 pinned]; "Chunjom, Sikkim, 6800', 12.X.59, F. Schmid", 5 ♂ [1 on slide, 4 pinned]; paratypes deposited in CNC, BMNH, USNM, and GWC.

Derivation of specific epithet: From the Greek for "autumnal", in reference to the season when this species is active.

Distribution: Known only from the Himalaya of Sikkim and northern Assam (Fig. 81). The species presumably also occurs in adjacent regions of Bhutan and Nepal.

Bionomics: Type material was apparently collected from swarms near streams (Schmid 1988, *personal communication*). Collection records suggest that *D. oporina* is primarily a "Fall" species, temporally isolated from *D. brachyrhina*, but not *D. mirabilis*. Certain of the paratypes (*e.g.*, those from Ramtang, Sikkim, 13.X.59) were from samples containing both *D. oporina* and *D. mirabilis* (see below); it is unknown if both species were taken from the same swarms.

4.5.3.3 *Deuterophlebia inyoensis* Kennedy

(Figs. 4a, 5, 15, 28, 37, 39, 41, 56, 60, 64, 69, 75, 82)

Deuterophlebia sp., Shewell 1954: 204.
Deuterophlebia sp., Kennedy 1958: 203.
Deuterophlebia inyoensis Kennedy 1960: 192.

Diagnosis. Larva similar to *D. shasta*, but recognized by the digitiform microtrichia on distal antennal article, and by sensilla *ap* (with two clusters of digitiform sensilla). Pupa similar to several species (*e.g.*, *D. coloradensis*), but distinguished by the gill (situated on ventrolateral protuberance) and abdominal microsculpture (microtubercles with dense apical microtrichia). Male readily separated from other species by the elongate median clypeal lobe, and by postgenal vestiture, antennal structure (sensilla (f1-3) not borne on tubercle), and dorsal plate shape (posterior margin truncate or only shallowly emarginate). Female distinguished from other species by postgenal vestiture, length of hind tarsomere 1 (length of t1/t5 greater than .6), and genital fork shape (anterior bridge extended less than half the distance to accessory gland opening).

Description

Larva (Fig. 5): Dorsal color: body light- or dark brown medially; mesothorax dark brown; proleg basally pale, distally grey to black. Dorsal cranium (instar IV), including clypeus and mandible base, dark brown. Distal antennal article relatively dark, with digitiform microtrichia (Fig. 39); pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (as in Fig. 3), *pm* (as in Fig. 10), *at* and *mt* (Fig. 4a) simple setiform sensilla; *sbt* (meso- and metathorax) lanciform sensilla (as in Fig. 10); *ap* with two setiform sensilla and two clusters of several digitiform sensilla (Fig. 4a). Measurements:

Instar	Sample size	Total length (mm)	Cranial width (mm)	Crochet rows	Antennal ratio
I	50	0.6-1.2 (0.87±0.13)	0.12-0.20 (0.17±0.02)	1	0:2:1
II	50	0.9-1.9 (1.37±0.26)	0.24-0.32 (0.26±0.02)	3	1:11:5
III	50	1.4-3.3 (2.26±0.44)	0.38-0.48 (0.43±0.02)	5-8	1:7:3
IV	50	2.3-4.9 (3.91±0.57)	0.60-0.72 (0.66±0.03)	7-12	1:3:1

Pupa (Fig. 15): Male antennal sheath coiled around periphery of ventral abdomen twice, terminated near posterior or lateral margin of abdomen. Gill base length subequal to width, on ventrolateral protuberance on margin of mesothorax (Fig. 28); gill filaments three in number, middle filament most closely associated with posterior filament. Thoracic tubercle on margin of anterolateral mesonotum, dorsad and slightly posterior to gill base; tubercle conical, darkly sclerotized apically in some specimens, but without spines. Mesonotal bands transverse, raised, darkly sclerotized, between thoracic tubercle and ecdysial line. In some specimens (*e.g.*, large male pupae), mesonotum with one pair of small, raised, darkly sclerotized dots anterodorsally. Metanotal bands similar to mesonotal bands, but less darkly sclerotized and shorter. Abdominal segments I, II, VI and VII laterally with 8-10, 12-18, 5-8 and 8-12 thorn-like spines, respectively.

Microsculpture: Mesonotum markedly rugose; meso- and metanotum irregularly set with ovoid microtubercles bearing apical microtrichia. Abdominal sutures simple, without secondary ridges; tergites with microtubercles (Fig. 41) bearing dense apical microtrichia; adjacent cuticle glabrous.

Measurements. Male pupae (N=114): Total length 2.8-3.8mm (3.28±0.23), width 2.0-2.5mm (2.22±0.12). Female pupae (N=92): Total length 2.8-3.8mm (3.13±0.23), width 1.9-2.5mm (2.13±0.14).

Adult ♂: Median clypeal lobe elongate, *ca.* 80μm long, apically truncate (Fig. 56), and with *ca.* 35 setiform sensilla; lateral lobes slightly developed, with sparse microtrichia. Anterior tentorial pits lateral to clypeal sensilla, *ca.* 40μm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture indistinct; postgena and oral region with microtrichia; mental tooth acute (Fig. 56). Each of antennal f1, f2 and f3 distally with a cluster of 6-9 digitiform sensilla, not borne on anteroventral tubercle (Fig. 60). Coxa, trochanter and [basal] femur with simple macrotrichia. Foretibia distally with capitate macrotrichia only on ventral margin (Fig. 64). Midtibia vestiture similar, but capitate macrotrichia present on dorsal margin of distal tibia. Hind tibia sparsely set with simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin, sparsely distributed distally on dorsal margin. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate (Fig. 75) subquadrate; posterior margin truncate or shallowly emarginate, and set with setiform sensilla. Gonostylus length subequal to length of dorsal plate, less than length of aedeagal sheath. Aedeagus internally smooth.

Measurements (N=10): Total body length 2.2-2.8mm (2.42±0.22). Antennal length 10.2-12.2mm (11.41±0.75); article length ratio 2.5:1:4:1.5:1.5:150. Wing length 4.6-5.2mm (4.88±0.19), width 2.1-2.4mm (2.19±0.10). Leg article percentages: foreleg - 5:4:24:36:16:5:5:4:3; midleg - 7:4:26:29:17:5:5:4:3; hindleg - 7:5:31:34:8:4:4:3:3.

Adult ♀: Similar to male. Median clypeal lobe convex, *ca.* 50μm long, with 15-30 setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca.* 40μm posterior to clypeal incision. Antennal pedicel with *ca.* five setiform sensilla; f1-4 narrow basally, expanded distally; each of f1-3 distally with anteroventral prominence bearing 1-3, 2-3, and 3-4 digitiform sensilla, respectively; f4 with 3-4 setiform sensilla and, anteroventrally, 1-2 digitiform sensilla.

Terminalia: Anterior bridge of genital fork extended posteriorly to less than half the distance to accessory gland opening (Fig. 37). Cercus with length of basal and distal article subequal; articles indistinctly fused to each other, separated only by indistinct, ventrolateral notch (as in Fig. 72).

Measurements (N=5): Total body length 2.2-2.4mm (2.29±0.11). Antennal length 0.43-0.46mm (0.44±0.01); article length ratio 3.5:1.5:4.5:1:1.5:2.5. Wing length 4.2-4.5mm (4.31±0.13), width 1.6-1.8mm (1.76±0.08). Leg article percentages: foreleg - 7:4:24:41:8:2:3:3:8; midleg - 7:4:25:40:8:2:3:4:9; hindleg - 8:4:28:38:6:3:3:3:7. Length of t1/t5: foreleg - .83-1.08 (.92±.10); midleg - .75-1.00 (.86±.09); hindleg - .67-.91 (.79±.11).

Egg: Extracted from immature pupae - white, circular, 0.16-0.18mm diameter; from mature pupae or adults - yellow, ovoid, 0.28-0.34mm in length, 0.12-0.14mm in width.

Holotype ♂[1]: USA, California, Mono Co., Lake Witsanapah (inlet), 37°31'N 118°52'W 3230m, 17.VIII.1954 (*H.D. Kennedy*); deposited in USNM (Kennedy 1988, *personal communication*)

Collection localities[2]: **Canada**; ALBERTA: Trans-Canada Hwy: Moraine Ck (Banff NP), 51°23'N 116°06'W 1505m; Yellowhead Hwy: Miette R (ca 1.5km below confl Meadow Ck), 52°51'N 118°13'W 1060m; Rocky Mountain Parks: Helen Ck (Banff NP), 51°39'N 116°22'W 1980m; Whistlers Ck (@ Wapiti C.G., Jasper NP), 52°49'N 118°03'W 1065m; Cavell Ck (below Teahouse, Jasper NP), 52°41'N 118°03'W 1770m; Cavell Ck (nr Angel Glacier, Jasper NP), 52°41'N 118°03'W 1980m; Maligne R (below Medicine Lk, Jasper NP), 52°54'N 117°56'W 1280m; Verdant Ck (Tonquin Valley, Jasper

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[1] Specimen not examined.

[2] Material examined from most localities listed.

NP), 52°54'N 118°07'W 1830m; BRITISH COLUMBIA: Trans-Canada Hwy: Emory Ck (N of Hope), 49°30'N 121°25'W 60m; ? Ck (Fraser R Valley, below Thompsons Bridge); Camp Ck (nr Camp Lake), 50°58'N 118°31'W 455m; Yard Ck ? (5mi W of "Last Spike", Sicamous), 50°54'N 118°48'W 380m; Victor Ck (@ Provincial Park), 50°57'N 118°24'W 550m; Loop Ck ? (Glacier NP), 51°15'N 117°32'W 1130m; Bostock Ck (7mi W of Rogers Pass), 51°13'N 117°40'W 945m; Klondike Hwy: Paddy Pass Ck (km 64.5), 59°53'N 134°47'W 810m; Trib., Tutshi Lake (km 66), 59°54'N 134°47'W 810m; Haines Hwy: Seltat Ck (km 81), 59°30'N 136°28'W 395m; Stonehouse Ck (km 89.5), 59°38'N 136°28'W 900m; Dick Ck (nr confl Stonehouse Ck), 59°38'N 136°28'W 900m; Tatshenshini Ck (= Goat Ck); Yellowhead Hwy: Grant Brook (@ Hwy Xing), 53°54'N 118°44'W 1060m; Moose R (@ Hwy Xing), 52°55'N 118°48'W 1040m; ? Ck (Mount Robson Provincial Park), 53°00'N 119°02'W 1065m; Kenneth Ck (ca 75km S of Prince George), 53°55'N 121°45'W 640m; ? Ck (50mi E of Prince Rupert); Hwy 5: Blue R (just below Hwy Xing), 52°07'N 119°18'W 675m; Finn Ck (S of Blue R), 51°55'N 119°09'W 640m; Cassiar Hwy: Packer Tom Ck (km 557), 58°53'N 130°02'W 775m; Bella Coola Hwy: Snootli Ck (@ Hwy Xing); Silverhope Creek Road: Eureka Ck (*ca.* 3.5km S of Hope), 49°20'N 121°28'W 150m; Silverhope Ck (*ca.* 5km S of Hope), 49°20'N 121°27'W 185m; Sowerby Ck (S of Hope), 49°19'N 121°25'W 350m; Silverhope Ck (@ km 15), 49°16'N 121°23'W 365m; Telegraph Creek Rd: Tatsho Ck (7.1mi W of Dease Lake), 58°23'N 130°09'W 745m; Alaska Hwy: Partridge Ck (km 1185), 59°58'N 131°13'W 865m; Screw Ck (km 1194), 59°54'N 131°18'W 855m; Logjam Ck (km 1210), 59°54'N 131°22'W 850m; Crowsnest Hwy: Wells Gray Rd: Spahats Ck (@ Provincial Park), 51°44'N 120°00'W; YUKON: Alaska Hwy: Boulder Ck (= Georges Gorge, km 1129), 60°05'N 130°23'W 885m; Canyon Ck (km 1146.5), 60°05'N 130°39'W 915m; Moore Ck (= Young Ck, km 1152.5), 60°05'N 130°44'W 915m; Seagull Ck (km 1180), 60°00'N 131°11'W 890m; Lone Tree Ck (km 1314), 60°16'N 132°58'W 700m; Campbell Hwy: Starr Ck (km 306.5), 61°46'N 131°51'W 840m; Railway Survey Ck (ca km 444), 62°10'N 134°05'W 685m; ? Ck (ca km 456), 62°11'N 134°17'W 635m; ? Ck (ca km 468), 62°11'N 134°31'W 610m; ? Ck (ca km 484), 62°12'N 134°46'W 610m; Dempster Hwy: Bensen Ck (km 28.5), 64°10'N 138°33'W 685m; ? Ck (km 39), 64°16'N 138°29'W 770m; Pea Soup Ck (km 40.5), 64°16'N 138°29'W 775m; Scout Car Ck (km 47.5), 64°20'N 138°26'W 855m; Wolfe Ck (km 50.5), 64°21'N 138°24'W 875m; N Fk Klondike R (km 56.5), 64°23'N 138°19'W 890m; Grizzly Ck (km 59), 64°24'N 138°18'W 930m; N Fk Klondike R (km 64.5), 64°26'N 138°14'W 940m; N Fk Klondike R (@ Hwy Xing, km 68), 64°28'N 138°11'W 995m; N Fk Klondike R (@ C.G., km 72.5), 64°30'N 138°13'W 1035m; Two Forks Site (km 78.5), 64°32'N 138°13'W 1220m; Engineer Ck (ca km 175), 65°09'N 138°23'W 750m; South Canol Rd: Rose R (km 150), 61°32'N 133°05'W 1020m; Upper Sheep Ck (@ Hwy Xing, km 156), 61°33'N 133°05'W 1065m; Upper Sheep Ck (Upper Sheep Ck Rd), 61°34'N 133°04'W 1080m; Pony Ck (km 160), 61°35'N 133°05'W 1090m; Groundhog Ck (km 166), 61°38'N 133°03'W 1085m; Trib., Lapie Lake (km 168), 61°39'N 133°02'W 1110m; Nahanni Range Rd: Long Lake Ck (km 35.5), 60°57'N 127°41'W 890m; South Branch Ck (km 53.5), 61°01'N 128°26'W 810m; Jackpine Ck (km 62), 61°05'N 128°23'W 780m; Spruce Ck (km 66.5), 61°07'N 128°22'W 780m; Conglomerate Ck (km 75), 61°11'N 128°19'W 780m; South Moose Ck (km 85), 61°16'N 128°17'W 820m; Tyers Pass [Flood] Ck (km 100.5), 61°23'N 128°15'W 860m; Hyland R (km 111.5), 61°29'N 128°13'W 850m; Ostensibility Ck (km 123.5), 61°34'N 128°18'W 880m; Piggott Ck (km 132), 61°39'N 128°18'W 930m; ? Ck (km 143.5), 61°43'N 128°18'W 1010m; ? Ck (km 147), 61°45'N 128°16'W 1030m; Hyland R (ca km 152), 61°48'N 128°17'W 1100m; Hyland R (ca km 167), 61°55'N 128°24'W 1190mm; Trib., Hyland R (ca km 167), 61°55'N 128°24'W 1190mm; Miscellaneous: Old Gold Ck (trib, Liard R), 60°57'N 130°45'W 885m; **United States**; ALASKA, Little Boulder Ck (ca 51km N of Haines), 59°25'N 136°07'W 130m; Yokeak Ck (= Big Boulder Ck, ca 55km N of Haines), 59°26'N 136°11'W 145m; "Carmack" Ck (ca 9km N of Skagway), 59°30'N 135°14'W 135m; CALIFORNIA, Eldorado Co.: Glen Alpine Ck (nr Fallen Leaf), 38°52'N 120°04'W 1980m; Inyo Co.: S Fk Big Pine Ck (1mi W of Glacier Lodge), 37°07'N 118°26'W 2440m; Trib., SW end Ruby Lake, 37°25'N 118°46'W 3370m; Madera Co.: Minaret Ck (below Falls), 37°38'N 119°05'W 2310m; Mono Co.: Convict Ck (upper), 37°31'N 118°52'W 3290m; Glacier Ck (@ Tioga Lake), 37°55'N 119°15'W 2985m; Lake Witsanapah (inlet), 37°31'N 118°52'W 3230m; Lee Vining Ck (@ Sawmill C.G.), 37°57'N 119°16'W 2965m; McGee Ck (upper), 37°29'N 118°50'W 3200m; Warren Fork (NE of Tioga Pass), 37°57'N 119°14'W 2865m; ? Ck (draining Hall Natural Area), 37°57'N 119°16'W 2970m; Shasta Co.: Kings Ck (Lassen Volcanic NP), 40°27'N 121°27'W 2210m; Siskiyou Co.: Fawn Ck (nr confl S Fk Sacramento R), 41°14'N 122°26'W 1460m; S Fk Sacramento R (@ F.S. Rd 26 Xing), 41°16'N 122°24'W 1120m; S Fk Sacramento R (nr confl Fawn Ck), 41°14'N 122°26'W 1460m; Gumboot Ck (@ F.S. Rd 26 Xing), 41°13'N 122°28'W 1615m; Trib., S Fk Sacramento R (along F.S. Rd 26), 41°15'N 122°25'W 1290m; Tuolumne Co.: Dana Fork (Yosemite NP), 37°53'N 119°16'W 2900m; Deadman Ck (SW of Sonora Pass), 38°19'N 119°39'W 2745m; MONTANA, Glacier Co.: Baring Ck (Glacier NP), 48°40'N 113°35'W 1415m; Siyeh Ck (Glacier NP), 48°42'N 113°40'W 1770m; ? Ck 5km SW Many Glacier (Glacier NP), 48°46'N 113°42'W 1705m; Ravalli Co.: Skalkalo Ck (Hwy 38 E of Grantsdale, approx), 46°09'N 114°00'W 1280m; OREGON, Clackamas Co.: Clackamas R (nr confl Roaring R), 45°09'N 122°06'W 295m; Roaring R (above C.G.), 45°09'N 122°06'W 295m; Sandy R (ca 1mi above confl Clear Ck), 45°21'N 121°55'W 460m; Douglas Co.: Watson Ck (below Falls), 43°14'N 122°23'W 830m; Hood River Co.: Polallie Ck (@ Hwy 35 Xing), 45°25'N 121°34'W 885m; Jackson Co.: Rogue R (@ Prospect), 42°44'N 122°29'W 595m; Klamath Co.: Trapper Ck (ca 0.5km above Odell Lk), 43°34'N 122°02'W 1465m; Lane Co.: Augusta Ck (along F.S. Rd 1927), 43°58'N 122°10'W 715m; French Pete Ck (above F.S. Rd 19 Xing), 44°01'N 122°12'W 560m; Mack Ck (H.J. Andrews Experimental Forest), 44°13'N 122°09'W 800m; Roaring R (@ C.G.), 43°57'N 122°05'W 790m; Roaring R (nr confl

McBee Ck), 43°56'N 122°04'W 965m; S Fk McKenzie R (nr confl Trail Ck), 44°00'N 122°10'W 620m; S Fk McKenzie R (@ Frissell Xing), 43°57'N 122°05'W 780m; Linn Co.: Hackleman Ck (@ Lost Prairie C.G.), 44°24'N 122°03'W 1005m; N Santiam R (3.9mi below Hwy 22 Xing), 44°33'N 121°59'W 885m; N Santiam R (@ Hwy 22 Xing), 44°30'N 122°00'W 1035m; Marion Co.: Clackamas R (@ F.S. Rd 46 Xing), 44°54'N 121°53'W 720m; French Ck (ca 0.5 mi above Detroit Res), 44°45'N 122°09'W 505m; Roaring Ck (Breitenbush sytem), 44°46'N 121°55'W 855m; Squirrel Ck (ca 0.5mi above confl Clackamas R), 44°52'N 121°50'W 1035m; Tunnel Ck (@ Hwy 22 Xing), 44°41'N 121°58'W 670m; Multnomah Co.: Wahkeena Ck (below Falls), 45°34'N 122°07'W 30-100m; WASHINGTON, Kittitas Co.: Rocky Run (?) Ck (1.3mi E Hyak), 47°23'N 121°22'W 790m; Klickitat Co.: Little Goose Ck (nr confl Smokey Ck), 46°03'N 121°40'W 930m; Trout Lk Ck (@ F.S. Rd 8810 Xing), 46°03'N 121°36'W 665m; White Salmon R (@ Trout Lk Xing), 46°00'N 121°31'W 595m; Lewis Co.: Chambers Ck (@ F.S. Rd 2160 Xing), 46°25'N 121°32'W 975m; Johnson Ck (@ F.S. Rd 2140 Xing), 46°29'N 121°34'W 790m; Nickel Ck (Ranier NP), 46°45'N 121°37'W 890m; Okanogan Co.: Silver Star Ck (@ Hwy 20 Xing), 48°35'N 120°35'W 1050m; Pierce Co.: Deer Ck (Ranier NP), 46°49'N 121°31'W 1065m; Ohanapecosh R (nr confl Panther Ck), 46°47'N 121°33'W 685m; Panther Ck (nr confl Ohanapecosh R), 46°47'N 121°33'W 685m; Tenas Ck (nr Nisqually entrance, Ranier NP), 46°44'N 121°55'W 610m; Skagit Co.: Bacon Ck (nr confl East Fk), 48°39'N 121°25'W 245m; Granite Ck (@ Hwy 20 Xing), 48°37'N 120°50'W 1005m; Marble Ck (ca 0.5mi above confl Cascade R), 48°32'N 121°16'W 330m; Rocky Ck (@ Hwy 20 Xing), 48°30'N 121°29'W 110m; Swamp Ck (@ Hwy 20 Xing), 48°33'N 120°46'W 1230m; Skamania Co.: Cispus R (@ F.S. Rd 23 Xing), 46°21'N 121°43'W 565m; Dog Ck (above Hwy 12 Xing), 45°42'N 121°40'W 46m; E Canyon Ck (nr Summit Prairie Ck), 46°18'N 121°43'W 790m; Rush Ck (@ F.S. Rd 90 Xing), 46°04'N 121°55'W 400m; Yellowjacket Ck (@ F.S. Rd 2809 Xing), 46°21'N 121°51'W 620m; Snohomish Co.: Lost Ck (ca 0.5km above confl N Fk Sauk R), 48°05'N

121°18'W 580m; Perry Ck (@ Perry Ck C.G.), 48°04'N 121°30'W 535m; Stujack Ck (nr confl White Chuck R), 48°10'N 121°23'W 410m; Whatcom Co.: Anderson Ck, 48°54'N 121°42'W 610m; Bagley Ck (@ Hwy 542 Xing), 48°52'N 121°40'W 830m; Barometer Ck (@ F.S. Spur Rd 020 Xing), 48°53'N 121°44'W 640m; Colonial Ck (@ Hwy 20 Xing), 48°41'N 121°06'W 390m; Cornell Ck (@ Hwy 542 Xing), 48°53'N 121°57'W 270m; Creek, N Cascades Hwy (Hwy 20, @ ca mile 136.5), 48°42'N 120°59'W 610m; Deadhorse Ck (@ F.S. Rd 3907 Xing), 48°54'N 121°50'W 395m; Goodell Ck (@ Newhalem), 48°40'N 121°15'W 145m; Panther Ck (nr confl Ruby Ck), 48°42'N 120°58'W 505m; Pyramid Ck (@ Hwy 20 Xing), 350m; Ruby Ck (nr confl Panther Ck), 48°42'N 120°58'W 505m; Ruth Ck (ca 0.5mi above confl N Fk Nooksack R), 48°53'N 121°39'W 655m; Wells Ck (nr Falls), 48°51'N 121°45'W 825m.

Distribution: Widespread western Nearctic, from the Sierra Nevada of California, Cascade Range of Oregon and Washington, and several mountain ranges of British Columbia and the Yukon (Fig. 82). In the Rocky and Mackenzie Mountains, the species occurs from central Montana to the southern Yukon. The paucity of records from central and northern British Columbia probably reflects the inaccessibility of these areas, rather than an actual gap in the distribution of *D. inyoensis*.

Bionomics: *Deuterophlebia inyoensis* is probably the most stenobiontic Nearctic species, restricted primarily to small, stenothermal, torrential streams. The immature stages typically occur in habitats where current velocity exceeds 1.5m/s. At many sites, larvae and pupae coexist with the blephariceridš *Agathon aylmeri* (Garrett) and *A. comstocki* (Kellogg).

As in most species, *D. inyoensis* adults emerge early in the morning (0700-0800h), with the emergence period typically lasting *ca.* 1 hour. Flight behaviour of *D. inyoensis* is similar to other species, though adult activity is often comparatively higher over the stream. This may be an artifact of canopy cover, and its influence on sunlight penetration and the location of male swarms (see chapter 5). Live, wingless females have been collected in larval habitats, suggesting active oviposition on submerged substrates. Fecundity estimates ranged from 80-197 eggs / female pupa (140.7±25.6, N=34) and was correlated with pupal size (see chapter 5).

Seasonal activity of *D. inyoensis* is often early and sometimes quite synchronous, with larvae, pupae and adult present for only 2-3 months. The remainder of the year, including the overwintering period, is passed in the egg stage. Most populations are univoltine, though data from some populations suggest a small second generation is possible (see chapter 5).

Remarks: Shewell (1954) reported on the first mountain midge from Canada, a single pupa found in Cavell Creek, Jasper National Park, Alberta. Shewell remained uncommitted as to the specimen's identity, but included figures of *D. coloradensis* (after Pennak 1945) and stated that the Cavell pupa "agrees with the description of *D. coloradensis*" (pg. 205). This apparently led to the impression that the specimen was *D. coloradensis* (Mani 1962; Kennedy 1965; Turner, *et al.* 1986). Although *D. coloradensis* occurs in other streams in Jasper National Park (see later), all Cavell Creek specimens, including the one mentioned by Shewell, are *D. inyoensis*.

Kennedy (1958) referred to certain Sierra Nevada populations (upper Convict and McGee Creeks) simply as *Deuterophlebia* sp., in part because he believed these specimens may have represented a new species. Subsequently (Kennedy 1960), this material was included in his description of *D. inyoensis*.

Identification of deuterophlebiid larvae typically requires mature (instar IV) specimens. Although proleg structure is relatively constant between species, the presence of three rows of crochets on instar II *D. inyoensis* is unique among Nearctic species; all others species possess four rows of crochets. No instar I or III characters permit differentiation of Nearctic species.

Kennedy (1960), based primarily on specimens from the Sierra Nevada, considered the presence of small, dark, sclerotized dots on the pupal mesonotum (Fig. 15) a diagnostic feature of *D. inyoensis*. Examination of specimens from throughout western North America has demonstrated the inconsistency of this character (*personal observation*; Kennedy, 1983 *personal communication*). These sclerotized dots occur mostly on large pupae, suggesting the feature may be allometric. Discovery of large pupae of *D. personata*, *D. vernalis*, and *D. coloradensis* with similar sculpturing supports this hypothesis.

Deuterophlebia inyoensis is one of the most common and widespread Nearctic deuterophlebiids, and, depending on the locality, it may occur sympatrically with one or more species (*e.g.*, *D. coloradensis*, *D. shasta*, *D. personata*). However, semaphoronts are isolated temporally at most sites, with *D. inyoensis* active before other species.

4.5.3.4 *Deuterophlebia blepharis* sp. nov.

(Figs. 54, 81)

Diagnosis. Male and female both similar to *D. mirabilis*, but readily differentiated by vestiture on the compound eyes (microtrichia between eye facets).

Description

Larva: Unknown.

Pupa: Unknown.

Adult ♂: Median clypeal lobe convex, *ca.* 40μm in length, with *ca.* 20 setiform sensilla; lateral lobes pronounced, with dense microtrichia. Anterior tentorial pits *ca.* 70μm posterior to clypeal incision. Compound eyes with microtrichia surrounding eye facets (Fig. 54). Subgenal suture indistinct; postgena and oral region with microtrichia (as in Figs. 55, 56); mental tooth acute. Antennal f1 distally with small anteroventral tubercle bearing 9 digitiform sensilla; each of f2 and f3 distally with anteroventral tubercle bearing *ca.* five digitiform sensilla. Coxa, trochanter and femur sparsely set with macrotrichia; fore and middle tibia with simple macrotrichia, distally with abundant capitate macrotrichia, especially on ventral margin (as in Fig. 58). Hind tibia with simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin of distal tibia. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate with posterior margin shallowly emarginate, notched medially, and bearing chaetiform and setiform sensilla; posterolateral angle blunt; lateral margins parallel-sided. Gonostylus length greater than length of dorsal plate or aedeagal sheath. Aedeagus internally smooth.

Measurements (N=3): Total body length 2.0-2.9mm (2.37±0.48). Antennal length 12.4-12.7mm (12.51±0.20); article length ratio 3:1:3.5:1.5:1.5:175. Wing length 5.2-5.3mm (5.27±0.06), width 2.3-2.4mm (2.37±0.02). Leg article percentages: foreleg - 5:3:25:35:17:5:4:4:2; midleg - 8:4:26:29:18:5:4:3:3; hindleg - 7:4:33:36:7:4:4:3:2.

Adult ♀[1]: Similar to male. Median clypeal lobe slightly convex, 10μm long, with seven setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca.* 30μm posterior to clypeal incision. Antennal f1-4 narrow basally, expanded distally; each of f1-3 distally with slight anteroventral prominence bearing two, three, and three digitiform sensilla, respectively; f4 with four setiform sensilla and, anteroventrally, three digitiform sensilla.

Terminalia: Cercus with length of basal article greater than length of distal article; articles distinguishable by constriction on all but medial margin (as in Fig. 71).

Measurements: Total body length 2.3mm. Antennal length 0.50mm; article length ratio 2.5:1:3:1.5:2:3. Wing length 4.8mm, width 2.0mm. Leg article percentages: foreleg - 7:3:23:44:7:3:3:3:9; midleg - 6:4:26:40:6:3:3:3:10; hindleg - 8:4:28:39:4:3:3:3:8. Length of t1/t5: foreleg - .71; midleg - .62; hindleg - .58.

Holotype ♂: "Sikkim, Yangsap [ca. 27°28'N 88°07'E], 9-X-1959, F. Schmid"; specimen on 2 slides (in Canada Balsam); [CNC].

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[1] Female description based solely on allotype specimen.

Allotype ♀: Same data as holotype; specimen on slide (in Canada Balsam); [CNC].

Paratypes: Same data as holotype, 2♂ [pinned]; paratypes deposited in CNC.

Derivation of specific epithet: From the Greek for "eyelash", in reference to the microtrichia between the eye facets.

Distribution: Known only from Sikkim (Fig. 81).

Bionomics: *Deuterophlebia blepharis* apparently co-occurs with at least one other species, *D. mirabilis*. The *D. blepharis* type series was from a series of adults that included seven (6♂, 1 ♀) *D. mirabilis*. It is unknown if all were from the same habitat or swarm.

4.5.3.5 *Deuterophlebia mirabilis* Edwards

(Figs. 76, 81)

Deuterophlebia mirabilis Edwards, 1922: 382.

Diagnosis. Male similar to *D. blepharis* and *D. inyoensis*; distinguished from the former species by lack of vesititure on the compound eyes, and from *D. inyoensis* by the shape of the dorsal plate (*i.e.*, in *D. mirabilis*, the posterior margin of the dorsal plate bears a median notch) and presence of anteroventral tubercles on flagellomeres 1-3 (absent in *D. inyoensis*). Female: Similar to *D. blepharis* and *D. inyoensis*; separable from the former by lack of vesititure on the compound eyes, and from *D. inyoensis* by the relatively short hind tarsomere 1 (length of t1/t5 less than 0.6); distinguished from other species (*e.g.*, *D. shasta*) by the presence of microtrichia on the postgena and oral region.

Description

Larva: Unknown (not definitively associated with adult).

Pupa: Unknown (not definitively associated with adult).

Adult ♂: Median clypeal lobe apically convex, with length varied (30-60μm), bearing *ca*. 20 setiform sensilla; lateral lobes pronounced, densely set with microtrichia. Anterior tentorial pits *ca*. 60μm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture indistinct in most specimens; postgena and oral region with microtrichia (as in Fig. 55, 56); mental tooth acute. Antennal f1 distally with small anteroventral tubercle bearing 4-8 digitiform sensilla; each of f2 and f3 distally with anteroventral tubercle bearing 5-8 digitiform sensilla. Coxa, trochanter and femur with sparse macrotrichia; fore and middle tibia sparsely set with simple macrotrichia, distally with abundant capitate macrotrichia, especially on ventral margin (as in Fig. 58). Hind tibia with sparse simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin of distal tibia. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate (Fig. 76) with posterior margin shallowly emarginate, notched medially, and bearing chaetiform and setiform sensilla; posterolateral angle acute; lateral margins parallel-sided to slightly concave. Gonostylus length less than length of dorsal plate, greater than length of aedeagal sheath. Aedeagus internally smooth.

Measurements (N=11): Total body length 2.1-3.1mm (2.66±0.28). Antennal length 9.6-13.4mm (11.67±1.11); article length ratio 3:1:4:2:2:170. Wing length 4.2-6.0mm (5.11±0.55), width 2.0-2.9mm (2.39±0.29). Leg article percentages: foreleg - 6:3:24:36:17:5:4:3:2; midleg - 8:4:26:30:17:5:4:3:2; hindleg - 8:4:31:36:8:4:4:3:2.

Adult ♀: Similar to male. Median clypeal lobe convex, *ca*. 40μm long, with *ca*. 10 setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca*. 45μm posterior to clypeal incision. Antennal f1-4 narrow basally, expanded distally; each of f1-3 distally with slight anteroventral prominence bearing 0-2, 3-5, and 4-10 digitiform sensilla, respectively; f4 with four setiform sensilla and, anteroventrally, five digitiform sensilla.

Terminalia: Anterior bridge of genital fork extended posteriorly to more than half the distance to accessory gland opening. Cercus with length of basal article less than length of distal article; articles indistinctly fused to each other, with the point of fusion not marked by an obvious constriction (as in Fig. 70).

Measurements (N=4): Total body length 2.4-2.6mm (2.47±0.02). Antennal length 0.50-0.54mm (0.52±0.02); article length ratio 2:1:3:1.5:2:1.5. Wing length 5.2-5.6mm (5.40±0.20), width. 2.0-2.2mm (2.12±0.12). Leg article percentages: foreleg - 6:3:22:42:6:3:4:3:11; midleg - 7:3:22:41:6:3:3:3:11; hindleg - 8:3:26:40:4:3:3:3:10. Length of t1/t5: foreleg - .58-.63 (.60±.02); midleg - .56-.67 (.60±.06); hindleg - .35-.47 (.40±.06).

Holotype: See below.

Lectotype Designation: The type series of *D. mirabilis* contained two male imagos from Kashmir, both designated as cotypes by Edwards (1922). One specimen was mounted on a slide, while the other was stored in formalin. The slide-mounted specimen apparently has been lost (B.C. Townsend[1] 1988, *personal communication*). I hereby designate as lectotype the remaining imago; the specimen evidently had dried out at some stage (R.W. Crosskey[1] 1984, *personal communication*), was then rehydrated and placed in alcohol. The specimen now has been removed from alcohol, dissected, and slide-mounted in Canada Balsam [2 slides]. Each slide carries the following labels: "Kashmir, Srinagar, 11-12,000', 1921, coll. F.J. Mitchell, 414." and "LECTOTYPE; designated by G.W. Courtney 1989". The specimen is deposited in the BMNH.

Other material examined: "China, Ürümqui, Tienshan-Geb., ±2000m, Antg. Oktober 1984, Auf Schnee am Bachrand, lg. Dr. R. Lübenau-Nestle" 4♂ 3♀ [ZSM], 1♂ 1♀ [GWC]; "Pakistan (Chitral), Besti, 20-X-1954, F. Schmid", 2♂ [CNC]; "Sikkim, Chachu, 29.VI.1959, F.Schmid", 4♂ [CNC]; "Chunjom, Sikkim, 6800', 12.X.59, F. Schmid", 3 ♂ [CNC]; "Sikkim, Gopetang, 5780', 10-X-1959, F.Schmid", 12♂ 1♀

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[1] British Museum (Natural History), Cromwell Road, London SW7 5BD.

[CNC]; "Kalep, Sikkim, 12,100', 18.VI.59, F. Schmid", 20 ♂ [CNC]; "Lungthu Ridge, Sikkim, 3700m, 30.VIII.1959, F. Schmid", 8 ♂ [CNC];."Ramtang, Sikkim, 5780', 24.IV.59, F.Schmid", 31♂ [CNC]; "Ramtang, Sikkim, 5780', 13.X.59, F.Schmid", 14♂ [CNC]; "Tsomgo, Sikkim, 9900', 26.VIII.59, F. Schmid", 5 ♂ [CNC]; "Sikkim, Tangshing, 5-X-1959, F.Schmid", 8♂ 1♀ [CNC]; "Sikkim, Tangshing, 12,200', 7-X-1959, F.Schmid", 2♂ [CNC]; "Sikkim, Yangsap, 9-X-1959, F. Schmid" 6♂ 1♀ [CNC].

Distribution: Apparently widespread in central Asia (Fig. 81), with most records from the Himalaya (Sikkim, India, and Pakistan) and Tien Shan (USSR and China). Also known from the Hindu Kush (northeast Afghanistan) (Tokunaga 1966), and may occur in parts of the Altai (Pulikovsky 1924; Brodsky 1930 (but see below)).

Bionomics: Collection records (*e.g.*, from Ramtang, Sikkim) suggest *D. mirabilis* may be bivoltine. Mani (1962) has suggested multiple generations for certain populations in the Himalaya. Alternatively, two species may be present. At present, however, adult characters provide no evidence of more than a single species.

Remarks: Brodsky (1930) provided relatively detailed descriptions of larvae, pupae, and pharate adults (dissected from pupae) from the Tien Shan, all of which were identified as *D. mirabilis*. Because I was unable to examine any of this material, and because he apparently collected two different species (see his discussion on pp.313-314), I have decided to refer to this material simply as *D.* sp.. Most of Brodsky's specimens indeed may represent *D. mirabilis*; however, until larvae, pupae, and female imagos have been definitively associated with the *D. mirabilis* type series, or at least with *D. mirabilis* males from nearer the type locality, it is preferable to call this material *D.* sp..

4.5.3.6 *Deuterophlebia nipponica* Kitakami

(Figs. 26, 81)

Deuterophlebia nipponica Kitakami, 1938b: 488.

Diagnosis. Pupa similar to several other species (*e.g.*, *D. coloradensis*), but recognized by the presence of three pairs of raised, darkly sclerotized mesonotal bands, and one pair of similar bands on each of abdominal segments I-VII. *Deuterophlebia bicarinata* sp. nov. (see below) has similar abdominal sculpturing, but only on segments I and II; these species are further separated on the basis of mesothoracic spines.

Description[1]

Larva: See Kitakami (1938b). [chaetotaxy could not be evaluated].

Pupa (Fig. 26)[2]. See Kitakami (1938b). Abdominal segments I-VII each with transverse, raised, darkly sclerotized bands on either side of midline, and small, raised, darkly sclerotized dots farther laterad. Microsculpture: Abdominal sutures with secondary ridges; tergites without microtubercles; microtrichia [apparently] absent.

Adult ♂: See Kitakami (1938b).

Adult ♀: See Kitakami (1938b). Postgenal vestiture absent.

Holotype: None designated.

Material examined: JAPAN, Kurama River near Kyoto, 23.X.1932 (*S. Kitakami*?) [1L, 1P] [USNM].

Distribution: Known only from Japan (islands of Honshû and Kyûshû) (Fig. 81).

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[1] Only two specimens were available for examination: one damaged larva and one partial pupa, the latter of which had been dissected; because of the lack of material, I refer to Kitakami (1938b) for most information.

[2] Because I was able to evaluate microsculptural features, a figure and partial description of the pupa is provided. Note that the specimen examined was a female that lacked its thorax; therefore, I provide no details about the gill or mesonotum, and rely on Kitakami (1938b) for certain key characters.

Bionomics: Yie (1933) gives a detailed account of the bionomics of *D. nipponica*. Populations near Kyoto [if they still exist!] apparently are multivoltine, and active through much of the year. Pupal collections consisting of predominantly females (Yie 1933; Kitakami 1938b) suggest the species may be parthenogenetic across most of its range.

4.5.3.7 *Deuterophlebia tyosenensis* Kitakami

(Figs. 24, 81)

Deuterophlebia tyosenensis Kitakami, 1938b: 501.

Diagnosis. Pupa readily separated from most species by the presence of two spines on each side of the mesothorax; similar to *D*. species C (from Nepal, see 4.5.3.15.3), but recognized by differences in size and abdominal microsculpture.

Description[1]

Larva: See Kitakami (1938b).

Pupa (Fig. 24)[2]: See Kitakami (1938b). Microsculpture: Abdominal sutures without secondary ridges; tergites without microtubercles; microtrichia [apparently] absent.

Adult: Unknown.

Holotype: None designated.

Material examined: One pupa: "Kurama River, Kyoto, JAPAN, 23.X.1932" [USNM]; the specimen is presumably not from Japan, but from Korea (Kitakami 1938b).

Distribution: Known from central and northern Korea (Kitakami 1938b) (Fig. 81).

Bionomics: Unknown.

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[1] Only a single, damaged pupa (female) was available for examination. Because of insufficient material for character evaluation, I refer to Kitakami (1938b) for most information.

[2] For reasons given above (*re. D. nipponica*), a figure and partial description of the pupa are provided.

4.5.3.8 *Deuterophlebia bicarinata* sp. nov.

(Figs. 9, 22, 27, 46, 81)

Diagnosis. Larva similar to *D. sajanica*, but differing in dorsal cranial color (clypeal lobe distally pale) and chaetotaxy (sensillum *pm* branched). Pupa similar to *D. sajanica*, but recognized by transverse, raised, darkly sclerotized bands on either side of abdominal segment I and II, and by microsculptural differences (*i.e.*, abdominal microtubercles concentrated near sutures in *D. bicarinata*). Adult male separable from most species by indistinct median clypeal lobe; imagos indistinguishable from *D. sajanica*.

Description

Larva (Fig. 9): Dorsal color: body pale to light brown. Dorsal cranium (instar IV) laterally pale, medially with broad, dark band extended from prothorax to clypeus; clypeal lobe dark at base, pale distally. Distal antennal article pale, without digitiform microtrichia; pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (as in Fig. 2), *pm* (Fig. 9), *at* and *mt* (as in Fig. 4b) branched setiform sensilla; *sbt* (meso- and metathorax) simple setiform sensilla (Fig. 9); *ap* with two clusters of digitiform sensilla (as in Fig. 4a).

Measurements, instar IV (N=10): Total length 3.0-3.8mm (3.41±0.28), cranial width 0.54-0.62mm (0.58±0.02); proleg with 7-12 crochet rows; antennal ratio 1:2:1.

Pupa (Fig. 22): Male antennal sheath coiled around periphery of ventral abdomen twice, terminated near head. Gill base thick, short, *ca.* twice as long as wide; gill with thick, posteriorly projected lobe or filament, and three elongate filaments, with two of the latter three (posterior-most pair) typically borne on a common base (Fig. 27). Spine-bearing tubercle on dorsal, anterolateral margin of mesonotum, dorsad and slightly posterior to gill base; spine finely tapered and elongate, its apex extended anteriorly to beyond outer margin of gill. Mesonotal bands transverse, raised, darkly sclerotized, between thoracic tubercle and ecdysial line; anterodorsal mesonotum with 1-2 small, raised, darkly sclerotized dots on either side of ecdysial line.. Metanotal bands similar to mesonotal bands, but less darkly sclerotized and shorter. Abdominal segments I and II each with transverse, raised, darkly sclerotized band on either side of midline (Fig. 22, arrowheads). Abdominal segments I, II, VI and VII laterally with 7-9, 10-15, 8-10 and 8-12 thorn-like spines, respectively.

Microsculpture: Mesonotum moderately rugose; meso- and metanotum densely set with microtubercles, but without associated microtrichia. Abdominal sutures without secondary ridges; tergites with microtubercles mostly near sutures; microtrichia generally distributed over tergite surface, not intimately associated with microtubercles (Fig. 46).

Measurements. Male pupae (N=4): Total length 2.2-2.6mm (2.39±0.15), width 1.5-1.9mm (1.69±0.16). Female pupae (N=5): Total length 2.0-2.4mm (2.25±0.16), width 1.5-1.8mm (1.65±0.13).

Adult ♂: Median clypeal lobe indistinct, slightly convex, with 15-20 setiform sensilla (as in Fig. 49); lateral lobes pronounced, densely set with microtrichia. Anterior tentorial pits *ca.* 20μm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture distinct; postgena and oral region glabrous, except for a few microtrichia and setiform sensilla near anterior clypeal margin (as in Fig. 31, 57); mental tooth acute. Antennal f1 slightly bulbous distally and with *ca.* 25 digitiform sensilla; each of f2 and f3 distally with anteroventral tubercle bearing *ca.* 10 digitiform sensilla. Coxa, trochanter and femur with simple macrotrichia; fore and middle tibia sparsely set with simple macrotrichia, distally with abundant capitate macrotrichia, especially on ventral margin (as in Fig. 58). Hind tibia densely set with simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin, sparsely distributed on distal part of dorsal margin. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate laterally concave, with posterior margin emarginate, medially notched, and set with setiform and chaetiform sensilla; posterolateral angle acute.

Gonostylus length greater than length of dorsal plate or aedeagal sheath. Aedeagus internally smooth.

Measurements (based on a single pharate adult dissected from pupa): Antennal length 9.8mm; article length ratio 2.5:1:3.5:1.5:1.5:155.

Adult ♀: Similar to male. Median clypeal lobe broadly truncate, *ca*. 20µm long, with 10-15 setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca*. 30µm posterior to clypeal incision. Antennal f1-4 narrow basally, expanded distally; each of f1-3 distally with slight anteroventral prominence bearing, respectively, two, four, and two digitiform sensilla; f4 with four setiform sensilla and, anteroventrally, four digitiform sensilla.

Terminalia: Anterior bridge of genital fork posteriorly acute, extended more than half the distance to accessory gland opening (as in Fig. 36). Cercus with length of basal article less than length of distal article; articles indistinctly fused to each other, separated only by indistinct, ventrolateral notch (as in Fig. 70).

Measurements (based on two pharate adults dissected from pupae): Antennal length 0.32-0.34mm; article length ratio 3:1:2.5:1:1:1. Length of t1/t5: foreleg - .56-.58; midleg - .52-.60; hindleg - .31-.40.

Holotype ♂ [dissected from pupa]: "Samjong (620m), Kayasan, Hapchon-gun, Kyongsangnam-do, Korea [ca. 35°30'N 128°00'E], 25-26.V.83, S. Uchida"; specimen on slide (in Canada Balsam); deposited in USNM.

Allotype ♀ [dissected from pupa]: same data as holotype; specimen on slide (in Canada Balsam); deposited in USNM.

Paratypes: same data as holotype, [10L, 7P]; deposited in USNM, GWC, PZW.

Derivation of specific epithet: From the Latin for ridge or keel, in reference to two pair of transverse, raised, darkly sclerotized bands on abdominal tergites I-II of the pupa

Distribution: Known only from South Korea (Fig. 81).

Bionomics: Unknown.

4.5.3.9 *Deuterophlebia sajanica* Jedlicka and Halgos

(Figs. 23, 81)

Deuterophlebia sp. Pulikovsky, 1924: 45.

Deuterophlebia sajanica Jedlicka and Halgos, 1981: 973.

Diagnosis. Larva similar to *D. bicarinata*, but differing in dorsal cranial color (clypeal lobe dark) and chaetotaxy (sensilla *pm* setiform). Pupa similar to *D. bicarinata*, but differing in absence of transverse, darkly sclerotized bands on abdominal segments, and in microsculptural features (*i.e.*, abdominal microtubercles distributed generally over tergite surface). Adult male separable from most species by indistinct median clypeal lobe; imagos indistinguishable from *D. bicarinata*.

Description

Larva: See Jedlicka and Halgos (1981). Dorsal color: body pale to light brown. Dorsal cranium (instar IV) laterally pale, medially with broad, dark band extended from prothorax to clypeus; clypeal lobe dark. Distal antennal article pale, without digitiform microtrichia; pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (as in Fig. 2), *at* and *mt* (as in Fig. 4b) branched setiform sensilla; *pm* simple setiform sensilla (as in Fig. 10); *sbt* (meso- and metathorax) lanciform sensilla (as in Fig. 10); *ap* with two clusters of digitiform sensilla (as in Fig. 4a).

Measurements, instar IV (N=3): Total length 3.0-4.7mm (3.61±0.97), cranial width 0.62-0.64mm (0.63±0.01); proleg with 7-11 crochet rows; antennal ratio 1:2:1.

Pupa (Fig. 23): See Jedlicka and Halgos (1981). Gill base thick, short, *ca.* twice as long as wide; gill with thick, posteriorly projected lobe or filament, and three elongate filaments, with two of the latter three (posterior-most pair) typically borne on a common base (as in Fig. 27). Microsculpture: Mesonotum moderately glabrous; meso- and metanotum densely set with microtubercles, but without basal microtrichia. Abdominal sutures without secondary ridges; microtubercles and microtrichia generally distributed over tergite surface; microtrichia not intimately associated with microtubercles (as in Fig. 46).

Measurements. Male pupae (N=5): Total length 2.5-3.3mm (2.97±0.31), width 1.8-2.3mm (2.10±0.21). Female pupae (N=3): Total length 2.7-2.8mm (2.77±0.05), width 2.0mm.

Adult ♂: See Jedlicka and Halgos (1981). Median clypeal lobe indistinct, slightly convex (as in Fig. 49); lateral lobes pronounced, densely set with microtrichia. Anterior tentorial pits *ca.* 20μm posterior to clypeal incision. Subgenal suture distinct; postgena and oral region glabrous, but few microtrichia and setiform sensilla near anterior clypeal margin (as in Figs. 31, 57); mental tooth acute.

Terminalia: Gonostylus length greater than length of dorsal plate or aedeagal sheath. Aedeagus internally smooth.

Measurements[1]: Antennal length 7.5mm (11.7mm); article length ratio 2.5:1:3.5:1.5:1.5:120 (2.5:1:4.5:2:2:185).

Adult ♀: See Jedlicka and Halgos (1981). Median clypeal lobe broadly truncate, *ca.* 20μm long, with 10-15 setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca.* 30μm posterior to clypeal incision.

Terminalia: Anterior bridge of genital fork posteriorly acute, extended more than half the distance to accessory gland opening (as in Fig. 36). Cercus with length of basal and distal article subequal; articles indistinctly fused to each other, separated only by indistinct, ventrolateral notch (as in Fig. 72).

Measurements[2]: Antennal length 0.45mm; article length ratio 3.5:1:2:1:1:1. Length of t1/t5: foreleg - .39-.41; midleg - .38-.44; hindleg - .26-.30.

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[1] From Jedlicka and Halgos (1981) or personal observation (pharate adult dissected from a pupa; given in parentheses).

[2] From Jedlicka and Halgos (1981) or personal observations (two pharate adults dissected from pupae).

Holotype ♂ [dissected from pupa][1]: MONGOLIA, Chövsgöl ajmak, Ich-Chorogol, 1650m [ca. 51°30'N 100°30'E], 11.VIII.1976 (*L. Jedlicka* & *J. Halgos*); deposited in Slovak National Museum, Bratislava, Czechoslovakia, Type No.265.

Material examined: MONGOLIA, Chovd ajmak, 40km NW Duut sum, Dund gol nr Ulin Davaa, 23.VII.80, L. Jedlicka [1L, 7P (4♂/3♀)] [GWC, PZW]; USSR, [ca. 49°N 85°E] "Katen-Karagai, Buchtarma valley / South Altai / 23/VII-16., B. Schwanwitsch" [2L, 1P(♂)] [BMNH].

Distribution: Known from the Altai and Sayan Mountains of the USSR and western Mongolia (Fig. 81). The species' distribution in Mongolia was summarized by Jedlicka and Halgos (1985).

Bionomics: Pulikovsky (1924) provided a brief account of the habitat and behaviour of the species; otherwise, bionomical data are unknown.

4.5.3.10 *Deuterophlebia shasta* Wirth

(Figs. 3, 16, 40, 51, 67, 68, 83)

Deuterophlebia shasta Wirth 1951: 51.

Diagnosis. Larva similar to *D. inyoensis*, but recognized by the lack of digitiform microtrichia on distal antennal article and by the structure of sensilla *ap* (with only two digitiform sensilla). Pupa similar to *D. personata* but with microsculptural differences (abdominal sutures with secondary ridges, and abdominal microtubercles absent). Male readily separated from other species by the internally ridged aedeagus. Female difficult to distinguish from some species, but lack of postgenal vestiture, the short hind tarsomere 1

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[1] Specimen not examined.

(length of t1/t5 less than .6), and structure of cerci (length of basal article less than length of distal article) help identify the species.

Description

Larva (Fig. 3): Dorsal color: body light brown medially; mesothorax dark brown laterally; proleg pale, except for thin, grey band distally. Dorsal cranium (instar IV) anteriorly dark, in a region delimited posteriorly by antennal bases (and including clypeal lobe), and posteriorly pale, (or) dorsal cranium completely dark, but noticeably darker anterior to level of antennal base. Distal antennal article pale to slightly gray, without digitiform microtrichia; pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (Fig. 3), *pm* (as in Fig. 10), *at* and *mt* (as in Fig. 4a) simple setiform sensilla; *sbt* (meso- and metathorax) lanciform sensilla (as in Fig. 10); *ap* with two setiform sensilla and two digitiform sensilla (as in Fig. 4b). Measurements:

Instar	Sample size	Total length (mm)	Cranial width (mm)	Crochet rows	Antennal ratio
I	3	0.7-1.0 (0.84±0.13)	0.16-0.18 (0.17±0.01)	1	0:2:1
II	35	0.9-1.7 (1.38±0.23)	0.24-0.28 (0.26±0.01)	4	1:10:4
III	50	1.3-3.0 (2.23±0.34)	0.36-0.44 (0.41±0.02)	6-8	1:5:2
IV	50	2.3-4.4 (3.34±0.55)	0.52-0.66 (0.59±0.03)	8-13	3:6:2

Pupa (Fig. 16): Male antennal sheath coiled around periphery of ventral abdomen twice, terminated near head. Gill base thick, short, *ca.* twice as long as wide; gill filaments three in number, middle filament most closely associated with posterior filament. Spine-bearing tubercle on dorsal, anterolateral margin of mesonotum, dorsad and slightly posterior to gill base; spine finely tapered and elongate, its apex extended anteriorly to beyond outer margin of gill. Mesonotal bands transverse, raised, darkly sclerotized, between thoracic tubercle and ecdysial line. Metanotal bands similar to mesonotal bands, but less darkly sclerotized and shorter. Abdominal segments I, II, VI and VII laterally with 8-10, 15-20, 7-10 and 10-15 thorn-like spines, respectively.

Microsculpture: Mesonotum moderately glabrous; meso- and metanotum without microtubercles, but irregularly set with microtrichia. Abdominal sutures with secondary ridges; tergites without microtubercles, but with clusters of microtrichia (Fig. 40).

Measurements. Male pupae (N=50): Total length 2.1-2.9mm (2.52±0.20), width 1.5-2.4mm (1.79±0.17). Female pupae (N=50): Total length 2.1-2.8mm (2.45±0.20), width 1.5-2.1mm (1.76±0.16).

Adult ♂: Median clypeal lobe of moderate length, *ca.* 50µm long, apically convex, with *ca.* 20 setiform sensilla (Fig. 51); lateral lobes pronounced, densely set with microtrichia. Anterior tentorial pits *ca.* 50µm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture distinct; postgena and oral region glabrous, but few microtrichia and setiform sensilla near anterior clypeal margin (as in Fig. 57); mental tooth slightly developed. Antennal f1 distally with small anteroventral tubercle bearing 4-5 digitiform sensilla; 1-2 similar sensilla slightly basad of tubercle; f2 and f3 distally with anteroventral tubercle bearing 5-8 digitiform sensilla. Coxa, trochanter and femur with simple macrotrichia; fore and middle tibia sparsely set with simple macrotrichia, distally with abundant capitate macrotrichia, especially on ventral margin (as in Fig. 58). Hind tibia densely set with simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin, sparsely distributed on distal part of dorsal margin. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate (Fig. 67) subquadrate; posterior margin emarginate, medially notched, and set with setiform and chaetiform sensilla; posterolateral angle broadly rounded; lateral margins concave. Gonostylus length subequal to or less than length of dorsal plate or aedeagal sheath. Aedeagus internally with numerous, subparallel ridges on ventral margin (Fig. 68).

Measurements (N=10): Total body length 1.9-2.4mm (2.23±0.16). Antennal length 9.4-11.4mm (10.42±0.53); article length ratio 2:1:3:1.5:1.5:120. Wing length 3.8-

4.7mm (4.29±0.33), width 1.9-2.2mm (2.03±0.08). Leg article percentages: foreleg - 7:4:23:35:17:5:5:3:3; midleg - 9:3:26:29:17:5:4:3:3; hindleg - 8:5:31:34:8:4:4:3:3.

Adult ♀: Similar to male. Median clypeal lobe convex, *ca.* 20µm long, with *ca.* 10 setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca.* 30µm posterior to clypeal incision. Antennal f1-4 narrow basally, expanded distally; each of f1-3 distally with slight anteroventral prominence bearing one, three , and three digitiform sensilla, respectively; f4 with three setiform sensilla and, anteroventrally, three digitiform sensilla.

Terminalia: Anterior bridge of genital fork posteriorly acute, extended more than half the distance to accessory gland opening (as in Fig. 36). Cercus with length of basal less than length of distal article; articles indistinctly fused to each other, with the point of fusion not marked by an obvious constriction (Fig. 70).

Measurements (N=2): Total body length 1.3-1.6mm. Antennal length 0.31mm; article length ratio 3:1:3.5:1:1:2. Wing length 2.7-2.9mm, width 1.2-1.3mm. Leg article percentages: foreleg - 7:4:23:41:4:3:4:4:11; midleg - 8:4:23:39:5:3:4:4:11; hindleg - 9:4:25:39:4:3:4:4:10. Length of t1/t5: foreleg - .36-.45; midleg - .43-.45; hindleg - .35-.39.

Egg: Extracted from immature pupae - white, circular, 0.14-0.18mm diameter; from mature pupae or adults - yellow, ovate, 0.24-0.26mm in length, 0.10-0.12mm in width.

Holotype ♂ [dissected from pupa]: USA, California, Siskiyou Co., Fawn Creek near headwaters of S Fk Sacramento R, 41°14'N 122°26'W 1460m, 22.VII.1948 (*W. W. Wirth*); 4 slides; USNM Type No. 59,374.

Collection localities[1]: **United States;** CALIFORNIA, Del Norte Co.: Hardscrabble Ck (@ Hwy 99 Xing), 41°50'N 124°01'W 73m; M Fk Smith R (@ Panther Flat), 41°50'N 123°55'W 135m; M Fk Smith R (above Howard Griffin Bridge), 41°50'N

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[1] Material examined from most localities listed.

123°52'W 220m; M Fk Smith R (1.5mi above Siskiyou Fk Rd), 41°53'N 123°47'W 335m; Patrick Ck (0.8mi above confl M Fk Smith R), 41°52'N 123°51'W 265m; S Fk Smith R, 41°47'N 123°39'W 45m; S Fk Smith R (above Steven Memorial Bridge), 41°41'N 123°55'W 170m; Smith R (1.3mi below Hwy 199), 41°48'N 124°05'W 17m; Siskiyou Co.: Fawn Ck (nr confl S Fk Sacramento R), 41°14'N 122°26'W 1460m; S Fk Sacramento R (@ F.S. Rd 26 Xing), 41°16'N 122°24'W 1120m; S Fk Sacramento R (nr confl Fawn Ck), 41°14'N 122°26'W 1460m; OREGON, Curry Co.: Illinois R (@ Oak Flat), 42°30'N 124°02'W 46m; Lawson Ck (@ Oak Flat), 42°30'N 124°02'W 46m.

Distribution: Known from only two drainages in northern California (South Fork Sacramento River and Smith River (Del Norte Co.)) and one in southwestern Oregon Illinois River (Curry Co.) (Fig. 83).

Bionomics: Larval and pupal samples from the Middle Fork Smith River indicate that the Smith River population is active from early April to August and may pass through more than one annual generation. Other *D. shasta* populations are apparently univoltine. Adult behaviour is typical of other Nearctic species, including the occasional formation of large swarms above whitewater habitats. Fecundity estimates, based mostly on the Smith River population, ranged from 61-176 eggs / female pupa (111.8±35.7, N=18)

Remarks: *Deuterophlebia shasta* is reported to occur in Glen Alpine Creek, California (Kennedy 1960) and in tributaries of the Marys River, Oregon (Wirth, 1951). As discussed below, material from Glen Alpine Creek and the Marys River watershed are conspecific with *D. personata* sp. nov. and *D. coloradensis*, respectively.

Deuterophlebia shasta and *D. inyoensis* are sympatric, but temporally isolated (at least among semaphoronts) in the South Fork Sacramento River watershed. The activity period is mid-April to early July for *D. inyoensis*, and early June to August for *D. shasta*; adult *D. shasta* begin emerging in mid-July, subsequent to *D. inyoensis* activity. The *D. shasta* type series, collected on 22 July 1948, contained no *D. inyoensis* (*personal* *observation*). The Smith River drainage, on the northern California coast, and Lawson Creek, a tributary of the Illinois River in southwestern Oregon, contain only *D. shasta*.

4.5.3.11 *Deuterophlebia personata* sp. nov.

(Figs. 1, 11-14, 43, 52, 58, 72, 78, 83)

Deuterophlebia sp. Kennedy 1958: 202.

Deuterophlebia shasta Kennedy 1960: 191.

Diagnosis. Larva similar to *D. shasta*, but differing in chaetotaxy (sensilla *prl*, *at*, *mt* branched) and antennal article proportions (1:2:1); differs from *D. coloradensis* in having a dark clypeal lobe; separated from *D. vernalis* by cranial color pattern. Pupa similar to *D. shasta*, but with microsculptural differences (abdominal microtubercles present, abdominal sutures without secondary ridges); separated from *D. bicarinata* and *D. sajanica* in having a three-filamented gill. Adults similar to *D. coloradensis*, but separated by genitalic characters (shape of dorsal plate in male; female cercus with articles indistinctly fused to each other).

Description

Larva (Fig. 1): Dorsal color: body pale to light brown medially; prolegs pale. Dorsal cranial color (instar IV): clypeus and mandible base covered by dark rectangular patch; posteriorly, either pale, or [in most populations] with dark, mask-like patch extended between, and covering, stemmata. Distal antennal article pale, without digitiform microtrichia; pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (as in Fig. 2), *at* and *mt* (as in Fig. 4b) branched setiform sensilla; *pm* simple setiform sensilla (as in

Fig. 10); *sbt* (meso- and metathorax) lanciform sensilla (as in Fig. 10); *ap* with two digitiform and two setiform sensilla (as in Fig. 4b). Measurements:

Instar	Sample size	Total length (mm)	Cranial width (mm)	Crochet rows	Antennal ratio
I	18	0.7-1.2 (0.89±0.13)	0.14-0.18 (0.16±0.02)	1	0:2:1
II	27	1.2-1.9 (1.51±0.17)	0.24-0.30 (0.27±0.01)	4	1:10:6
III	50	1.6-3.2 (2.57±0.37)	0.40-0.48 (0.44±0.02)	5-7	1:5:3
IV	50	3.1-5.2 (4.22±0.57)	0.62-0.70 (0.67±0.02)	7-12	1:2:1

Pupa (Figs. 13, 14): Male antennal sheath coiled around periphery of ventral abdomen twice, terminated near head. Gill base thick, short, *ca.* twice as wide as long; gill filaments three in number, middle filament most closely associated with posterior filament. Spine-bearing tubercle on dorsal, anterolateral margin of mesonotum, dorsad and slightly posterior to gill base; spine elongate, its apex extended anteriorly to near outer margin of gill. Mesonotal bands transverse, raised, darkly sclerotized, between thoracic tubercle and ecdysial line. In some specimens (*e.g.*, large male pupae) mesonotum with 1 pair of small, raised, darkly sclerotized dots anterodorsally. Metanotal bands similar to mesonotal bands, but less darkly sclerotized and shorter. Abdominal segments I, II, VI and VII laterally with 5-8, 7-10, 4-5 and 6-8 thorn-like spines, respectively.

Microsculpture: Meso- and metanotum irregularly set with ovoid microtubercles and associated basal microtrichia. Abdominal sutures simple, without secondary ridges; tergites with microtubercles; associated basal microtrichia of moderate length, extended radially to margins of adjacent microtubercles; microtubercles and surrounding cuticle glabrous (Fig. 43).

Measurements. Male pupae (N=75): Total length 2.6-3.4mm (3.12±0.17), width 1.8-2.4mm (2.12±0.12). Female pupae (N=75): Total length 2.2-3.4mm (3.03±0.21), width 1.6-2.4mm (2.05±0.15).

Adult ♂: Median clypeal lobe pronounced, broadly convex, *ca.* 30μm long, with *ca.* 35 setiform sensilla (Fig. 52); lateral lobes pronounced, densely set with microtrichia.

Anterior tentorial pits *ca.* 70µm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture distinct; postgena and oral region glabrous, but few microtrichia and setiform sensilla on ventral apex of median clypeal lobe (as in Fig. 57); mental tooth acute. Antennal f1 distally with small anteroventral tubercle bearing 4-6 digitiform sensilla; 1-2 similar sensilla slightly basad of tubercle (as in Fig. 33); f2 and f3 distally with anteroventral tubercle bearing 6-9 digitiform sensilla. Coxa, trochanter and femur with simple macrotrichia; fore and middle tibia sparsely set with simple macrotrichia, distally with abundant capitate macrotrichia, especially on ventral margin (Fig. 58). Hind tibia densely set with simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin, sparsely distributed on distal part of dorsal margin. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate subquadrate; posterior margin slightly emarginate, medially notched (Fig. 78), and set with setiform and chaetiform sensilla. Gonostylus longer than dorsal plate or aedeagal sheath, as long as dorsal margin of gonocoxite. Aedeagus internally smooth.

Measurements (N=10): Total body length 2.3-2.8mm (2.38±0.29). Antennal length 10.3-11.3mm (10.84±0.30); article length ratio 3:1:4:2:2:130. Wing length 4.4-5.0mm (4.76±0.18), width 2.0-2.5mm (2.19±0.20). Leg article percentages: foreleg - 5:3:24:35:17:5:5:3:3; midleg - 7:4:27:30:17:5:5:4:3; hindleg - 7:5:31:35:8:4:4:3:3.

Adult ♀: Similar to male. Median clypeal lobe broadly truncate, *ca.* 30µm long, with 10-20 setiform sensilla; clypeus laterally without pronounced lobes or dense microtrichia. Anterior tentorial pits *ca.* 35µm posterior to clypeal incision. Antennal pedicel with *ca.* five setiform sensilla; f1-4 narrow basally, expanded distally; each of f1-3 distally with slight anteroventral prominence bearing 1-2, 2-3, and 2-3 digitiform sensilla, respectively; f4 with 4 setiform sensilla and, anteroventrally, 3-5 digitiform sensilla.

Terminalia: Anterior bridge of genital fork extended posteriorly to more than half the distance to accessory gland opening (as in Fig. 36). Cercus with length of basal and distal article subequal; articles indistinctly fused to each other, separated only by indistinct, ventrolateral notch (Fig. 72).

Measurements (N=10): Total body length 1.5-2.4mm (2.07±0.32). Antennal length 0.34-0.46mm (0.39±0.04); article length ratio 3:1:3:1:1:1.5. Wing length 3.1-4.4mm (3.79±0.53), width 1.3-1.8mm (1.62±0.21). Leg article percentages: foreleg - 7:4:23:42:7:2:3:3:10; midleg - 7:3:24:41:7:2:3:3:11; hindleg - 9:4:26:39:4:2:3:3:10. Length of t1/t5: foreleg - .50-1.0 (.70±.16); midleg - .42-.87 (.67±.16); hindleg - .31-.58 (.41±.09).

Egg: Extracted from immature pupae - white, circular, 0.14-0.18mm diameter; from mature pupae or adults - light green, ovoid, 0.26-0.30mm in length, 0.12-0.14mm in width.

Holotype ♀ (reared from pupa): "USA Or. Tillamook Co, Cedar Ck nr Hebo [ca. 1mi above fish hatchery], 45°13'N 123°50'N 91m, 14.V.86 coll. G.W. Courtney"; "reared in laboratory, emerged 19.V.85"; "crit. point dried from alcohol"; specimen on pin, with head capsule, genitalia, and pupal exuviae in glycerin; deposited in USNM.

Allotype ♂ (reared from pupa): same data as holotype, except emerged 20.V.85; specimen on pin, with head capsule and pupal exuviae in glycerin; deposited in USNM.

Paratypes: **United States**; OREGON, Tillamook Co.: Cedar Ck (@ fish hatchery), 45°12'N 123°50'W 23m, 25.IV.82 (*G.W. Courtney*) [5 L, 5 P], 9.V.84 [22 L, 35 P]; Cedar Ck nr Hebo [ca. 1mi above fish hatchery], 45°13'N 123°50'W 91m, 14.V.86 (*G.W. Courtney*) [44 L, 13 P, 2 ♂ (reared), 1 ♀ (reared)], 28.V.86 [14 L, 3 P, 18 ♂, 2 ♀], 4.VI.86 [20 L, 11 P], 17.VI.86 [2 L, 1 P], 25.VI.86 [1 L, 1 P]; Three Rivers SE Hebo [nr confl Cedar Ck], 45°12'N 123°50'W 23m, 25.IV.82 (*G.W. Courtney*) [3 L, 3 P], 19.IV.85 [12 L, 1 P], 22.IV.86 [6 L, 9 P], 14.V.86 [4 P]; Three Rivers @ Castle Rock, 45°10'N 123°49'W 79m, 9.V.84 (*G.W. Courtney*) [1 P]. Paratypes deposited in BMNH, CNC, GWC, OrSU , USNM.

Other material examined: **Canada**; BRITISH COLUMBIA: [Silverhope Ck Rd] Eureka Ck 3.5km S of Hope, 49°20'N 121°28'W 150m, 1.VII.86 (*J.O. Lacoursière & D.C. Currie*) [1 P]; Silverhope Ck 15km S of Hope, 49°16'N 121°23'W 365m, 4.VIII.82 (*D.M. Wood*) [3 L, 18 P]; Sowerby Ck, Silver Lake Rd Xing, 49°19'N 121°25'W 350m, 28.VII.80 (*A. Borkent*) [2 L], 17.VII.88 (*G.W. Courtney*) [12 L, 13 P, 6 ♀ (reared)]; YUKON: Haines Hwy @ km 154, Tahkanne River, 60°06'N 136°56'W 715m, 23.VIII.84 (*G.W. Courtney*) [2 L, 4 P]; **United States**; CALIFORNIA, Eldorado Co.: Glen Alpine Ck nr Fallen Leaf, 38°52'N 120°04'W 1980m, 18.VII.85 (*G.W. Courtney*) [P exuviae], (*no date or collector*) [6 L, 11 P]; Grass Lake Ck [NW of Luther Pass], 38°47'N 120°00'W 2135m, 18.VII.85 (*G.W. Courtney*) [3 L, 22 P], 22.VII.85 (*G.W. Courtney*) [72 ♂, 19 ♀]; Madera Co.: Minaret Ck @ [Minaret] Falls, 37°38'N 119°05'W 2310m, 21.VII.85 (*G.W. Courtney*) [15 L, 8 P, 48 ♂, 12 ♀]; IDAHO, Boise Co.: Canyon Ck [nr confl S Fork Payette R], 44°10'N 115°14'W 1470m, 9.VIII.85 (*G.W. Courtney*) [2 P]; Canyon Ck [5mi above confl S Fork Payette R], 44°13'N 115°14'W 1755m, 9.VIII.85 (*G.W. Courtney*) [97 L, 2 P]; OREGON, Douglas Co.: Quines Ck above I-5 [Interstate Hwy 5] Xing, 42°46'N 123°16'W 475m, 26.IV.86 (*G.W. Courtney & M.J. Stansbury*) [1 L, 6 P]; Josephine Co.: Grave Ck @ I-5 [Interstate Hwy 5] Xing, 42°38'N 123°23'W 325m, 28.III.82 (*G.W. Courtney*) [3 L], 29.IV.84 [6 P], 5.V.86 [6 P], 10.V.86 [1 P], 22.III.86 (*G.W. Courtney & M.J. Stansbury*) [7 L, 3 P], 26.IV.86 [1 L, 1 P], 15.III.86 (*M.J. Stansbury*) [1 L], 29.III.86 [3 L, 3 P], 6.IV.86 [1 L, 5 P], 12.IV.86 [3 P], 20.IV.86 [1 L, 1 P], 3.V.86 [1 L], 18.V.86 [2 P]; Tillamook Co.: Cedar Ck (@ fish hatchery), 45°12'N 123°50'W 23m, 27.III.86 (*G.W. Courtney*) [18 L, 2 P], 2.IV.86 [11 L, 2 P], 8.IV.86 [33 L, 4 P], 16.IV.86 [16 L, 18 P], 30.IV.86 [12 L, 7 P], 7.V.86 [15 L, 4 P], 14.V.86 [15 L, 8 P], 28.V.86 [6 L, 10 P], 4.VI.86 [3 L, 10 P], 10.VI.86 [4 P]; Three Rivers @ Hebo, 45°13'N 123°51'W 12m, 13.III.86 (*G.W. Courtney*) [1 L], 19.III.86 [7 L]; Three Rivers SE Hebo [nr confl Cedar Ck], 45°12'N 123°50'W 23m, 6.III.86 (*G.W. Courtney*) [1 L]; WASHINGTON, Chelan Co.: Peshastin

Ck @ Negro Ck, 47°26'N 120°39'W 653m, 5.VII.83 (*G.W. Courtney*) [1 L, 4 P]; Lewis Co.: Clear Fork Cowlitz R @ La Wis Wis C.G., 46°40'N 121°34'W 385m, 19.VI.86 (*G.W. Courtney*) [19 L]; Johnson Ck above Hwy 12, 46°34'N 121°41'W 315m, 22.VI.81 (*N.H. Anderson & G.W. Courtney*) [3 L, 7 P], 19.VI.86 (*G.W. Courtney*) [15 L, 2 P]; Smith Ck above Hwy 12, 46°34'N 121°42'W 315m, 19.VI.86 (*G.W. Courtney*) [2 L, 1 P]; Okanogan Co.: Early Winters Ck nr Klipchuck [Xing], 48°35'N 120°30'W 830m, 16.VIII.85 (*G.W. Courtney*) [2 L, 2 P]; Early Winters Ck nr. confluence Silver Star Ck, 48°35'N 120°35'W 1030m, 16.VIII.85 (*G.W. Courtney*) [1 P]; Skagit Co.: Bacon Ck 1mi above confl Skagit River, 48°36'N 121°23'W 120m, 17.VIII.85 (*G.W. Courtney*) [1 L, 1 pupal exuvia]; Bacon Ck nr confl East Fk, 48°39'N 121°25'W 245m, 31.VII.86 (*G.W. Courtney*) [4 L, 1 P]; Marble Ck 0.5mi above confl Cascade R, 48°32'N 121°16'W 330m, 17.VIII.85 (*G.W. Courtney*) [10 L, 24 P], 30.VII.86 [63 L, 29 P]; Whatcom Co.: Panther Ck nr confl Ruby Ck, 48°42'N 120°58'W 505m, 16.VIII.85 (*G.W. Courtney*) [3 L, 2 P], 31.VII.86 [2 P]; Ruby Ck nr confl Panther Ck, 48°42'N 120°58'W 505m, 16.VIII.85 (*G.W. Courtney*) [4 L].

Derivation of specific epithet: From the Latin for masked, in reference to the color pattern on the larval cranium.

Distribution: Widespread western Nearctic, from the Sierra Nevada of California, to southwestern Yukon (Fig. 83). Because *D. personata* is unknown from northern and central British Columbia, the Yukon population may be a northern disjunction. However, inaccessibility of coastal ranges suggests that lack of records may be a collecting artifact.

Bionomics: The immature stages of *D. personata* inhabit a diversity of stream types, ranging from high-gradient, closed-canopy, 1st order streams, to low-gradient, exposed, 5th order rivers; most collections were from 3rd and 4th order streams in relatively steep, forested terrain.

Habitat characteristics for *D. personata* are similar to those of other deuterophlebiids, with immature stages typically inhabiting riffles where current velocities exceed 1m/s. All larval instars graze on the filamentous diatoms and periphyton on the upper and lateral surfaces of rocks. Pupae occur in the same microhabitat, usually in small cracks or depressions. Inhabited substrates vary, but sedimentary rocks, wood and vegetation are usually avoided. At many sites, the immature stages of *D. personata* co-occur with larvae and pupae of the blephariceridsbAgathon comstocki*, *A. aylmeri*, *Bibiocephala grandis* Osten Sacken, *Blepharicera jordani* Kellogg, and *Philorus californicus* Hogue.

Emergence characteristics of adult *D. personata* are similar to other Nearctic species, with all activity occurring early in the morning (*ca.* 0800-1000h). Upon emerging, male imagos fly back and forth in a zig-zag pattern, usually just above the stream surface and in an upstream direction. Large emergences often result in formation of male swarms over sunlit or whitewater reaches. Females typically fly alone, in a unidirectional path, and at heights that approximate the top of male swarms. At most sites, the flight period lasts *ca.* 30-45 minutes. As in most species (see below), female *D. personata* apparently oviposit on submerged substrates. Fecundity, estimated by pupal dissection and enumeration of eggs, ranged from 115 - 230 eggs / female (175.5±35.4, N=23) and was highly correlated with pupal size (see chapter 5).

Details of a phenological study of *D. personata* and other Nearctic mountain midges are provided elswhere (see chapter 5). Data for *D. personata* at the type locality indicate that the egg-hatching period extends from early March to late April, with adults emerging until *ca.* mid June. This population, and most others, are apparently univoltine, with most of the year passed in the egg stage.

Remarks: *Deuterophlebia personata* is sympatric with other deuterophlebiids over much of its range. The Sierra Nevada of California contains allopatric populations, and several populations where *D. personata* co-occurs with *D. coloradensis* and/or *D. inyoensis*. Kennedy (1960) referred to specimens from Glen Alpine Creek, near Lake Tahoe, as *D. shasta* , mostly because pupae had elongate mesothoracic spines. The present analysis has shown that spined Glen Alpine material belongs to *D. personata*. Other specimens from the Glen Alpine Creek include pupae which lack mesothoracic spines and are readily assignable to *D. inyoensis*. Minaret Creek, in the upper San Joaquin Valley, has the same sympatric combination, plus *D. coloradensis*. Pupal material from both Glen Alpine and Minaret Creeks suggests hybridization between *D. personata* and another species. Intermediate specimens, with a markedly rugose mesothorax, relatively elongate gill base, and short, irregularly shaped mesothoracic spines suggest hybridization between *D. personata* and *D. inyoensis*. Similar swarming, habitat and temporal characteristics further implicate this intergradation, rather than one involving *D. coloradensis*.

Additional support for this hybridization hypothesis comes from *D. personata* populations in Oregon, where sympatric cohabitants often include *D. coloradensis*, but not *D. inyoensis*. In Oregon, *D. inyoensis* is restricted to the Cascade Range and *D. personata* occurs only in coastal drainages; therefore, geographical overlap does not presently exist. Interestingly, Oregon populations of *D. personata* demonstrate less morphological variation and greater character consistency than Sierra Nevada populations. If, as suggested by California data, there is a tendency towards hybridization between *D. personata* and *D. inyoensis*, geographical isolation of these species may contribute to lower levels of character variation in Oregon populations of *D. personata*. In spite of varying amounts of habitat-, behavioural-, and temporal overlap, there is no evidence of hybridization between sympatric *D. personata* and *D. coloradensis*.

Deuterophlebia personata, *D. inyoensis*, and *D. coloradensis* are sympatric at several streams in the Cascade Range of Washington. At most sites, species are partially isolated temporally, with the typical sequence having *D. inyoensis* active early, followed by *D. personata*, then *D. coloradensis*. Still, there appears to be sufficient temporal overlap to permit hybridization opportunities, but, in contrast to sympatric populations in California, hybridization between *D. personata* and *D. inyoensis* is not suggested. Reproductive isolation of northern *D. personata* may be absolute, since all populations apparently are parthenogenetic. Sex ratios for *D. personata* populations, determined by enumerating pupae and instar IV larvae, demonstrate striking geographic variation. Samples from Washington, British Columbia, and the Yukon, representing 13 populations and 18 sample dates, consist entirely of females (N=228). These data provide compelling evidence that northern populations are parthenogenetic, and contrast dramatically with data for bisexual southern populations (Idaho, Oregon, California), where sex ratios are *ca.* equal (165 males : 166 females). At present, the mechanism of parthenogenesis is unknown.

4.5.3.12 *Deuterophlebia vernalis* sp. nov.

(Figs. 2, 4b, 18, 31-36, 45, 48, 57, 77, 83)

Diagnosis. Larva similar to *D. shasta*, but differing in chaetotaxy (sensilla *prl*, *at*, *mt* branched) and antennal article proportions (1:2:1); differs from *D. coloradensis* in possessing a dark clypeal lobe; separated from *D. personata* by cranial color pattern. Pupa similar to *D. coloradensis*, recognized by anal projection. Adults similar to *D. coloradensis*, but separated by dorsal plate shape (male) and length of t1/t5 (female).

Description

Larva (Fig.2): Dorsal color: body pale to light brown medially; prolegs pale. Dorsal cranial color (instar IV): mostly pale, with dark, medial, triangular patch, the base of which is delimited anteriorly by the clypeus and mandibles, and apex of which is extended posteriorly nearly to the prothorax. Distal antennal article pale, without digitiform microtrichia; pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (Fig. 2), *at* and *mt* (Fig. 4b) branched setiform sensilla; *pm* simple setiform sensilla (as in Fig. 10); *sbt* (meso- and metathorax) lanciform sensilla (as in Fig. 10); *ap* with two digitiform and two setiform sensilla (Fig. 4b). Measurements:

Instar	Sample size	Total length (mm)	Cranial width (mm)	Crochet rows	Antennal ratio
I	29	0.6-1.3 (1.00±0.16)	0.12-0.20 (0.18±0.02)	1	0:2:1
II	50	1.1-2.0 (1.58±0.20)	0.24-0.32 (0.29±0.01)	4	1:10:4
III	50	1.8-3.5 (2.86±0.43)	0.40-0.52 (0.45±0.02)	6-8	1:5:2
IV	50	3.0-5.1 (4.27±0.45)	0.60-0.72 (0.67±0.03)	8-13	1:2:1

Pupa (Fig. 18): Male antennal sheath coiled around periphery of ventral abdomen twice, terminated near head. Gill base thick, short, *ca.* twice as wide as long; gill filaments three in number, middle filament most closely associated with posterior filament. Thoracic tubercle on margin of anterolateral mesonotum, dorsad and slightly posterior to gill base; tubercle conical, darkly sclerotized apically in some specimens, but without spines. Mesonotal bands transverse, raised, darkly sclerotized, between thoracic tubercle and ecdysial line. In some specimens (*e.g.*, large male pupae), mesonotum with one pair of small, raised, darkly sclerotized dots anterodorsally. Metanotal bands similar to mesonotal bands, but less darkly sclerotized and shorter. Abdominal segments I, II, VI and VII laterally with 6-7, 10-14, 2-4 and 6-8 thorn-like spines, respectively. Segment IX posteromedially with anal projection (Fig. 48).

Microsculpture: Meso- and metanotum irregularly set with ovoid microtubercles and associated basal microtrichia. Abdominal sutures simple, without secondary ridges; tergites with microtubercles; associated basal microtrichia short, rarely extended radially to adjacent microtubercles; microtubercles and adjacent cuticle acinose (Fig. 45).

Measurements. Male pupae (N=128): Total length 2.7-3.3mm (2.72±0.12), width 1.9-2.4mm (2.17±0.09). Female pupae (N=111): Total length 2.3-3.0mm (2.70±0.12), width 1.8-2.3mm (2.03±0.10).

Adult ♂: Median lobe clypeal pronounced, broadly convex, *ca.* 30µm long, with *ca.* 50 setiform sensilla (Fig. 31); lateral lobes pronounced, densely set with microtrichia.

Anterior tentorial pits *ca.* 80µm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture distinct; postgena and oral region glabrous, but few microtrichia and setiform sensilla on ventral apex of median clypeal lobe (Fig. 57); mental tooth acute. Antennal f1 distally with small anteroventral tubercle bearing 5-7 digitiform sensilla; 2-3 similar sensilla proximal to tubercle (Fig. 33); f2 and f3 distally with anteroventral tubercle bearing 6-8 digitiform sensilla. Coxa, trochanter and femur with simple macrotrichia; fore and middle tibia sparsely set with simple macrotrichia, distally with abundant capitate macrotrichia, especially on ventral margin (as in Fig. 58). Hind tibia densely set with simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin, sparsely distributed on distal part of dorsal margin. All tarsi ventrally with capitate macrotrichia

Terminalia: Dorsal plate (Fig. 77) laterally concave, with posterior margin deeply emarginate, set with setiform and chaetiform sensilla. Gonostylus longer than dorsal plate or aedeagal sheath, as long as dorsal margin of gonocoxite. Aedeagus internally smooth.

Measurements (N=10): Total body length 2.0-2.7mm (2.41±0.20). Antennal length 10.8-12.8mm (11.83±0.73); article length ratio 2.5:1:4:1.5:1.5:140. Wing length 4.8-5.4mm (5.06±0.25), width 2.24-2.64mm (2.46±0.17). Leg article percentages: foreleg - 6:4:23:34:18:5:4:3:3; midleg - 8:4:26:29:17:5:4:3:3; hindleg - 7:5:30:35:8:4:4:3:3.

Adult ♀: Similar to male. Median clypeal lobe pronounced, convex, *ca.* 30µm long, with *ca.* 20 setiform sensilla (Fig. 32); clypeus laterally without pronounced lobes or dense microtrichia, though microtrichia often present near subgenal suture. Anterior tentorial pits *ca.* 30µm posterior to clypeal incision. Antennal pedicel with *ca.* six setiform sensilla; f1-4 narrow basally, expanded distally; each of f1-3 distally with slight anteroventral prominence bearing *ca.* three digitiform sensilla; f4 with six setiform sensilla, and, anteroventrally, 1-4 digitiform sensilla (Fig. 34).

Terminalia: Anterior bridge of genital fork posteriorly acute, extended more than half the distance to accessory gland opening.(Fig. 36). Cercus with length of basal article less than length of distal article; articles distinguishable by obvious constriction on all but medial margin (as in Fig. 71).

Measurements (N=10): Total body length 2.2-3.0mm (2.46±0.27). Antennal length 0.41-0.43mm (0.42±0.01); article length ratio 3.5:1:3:1:1:1.5. Wing length 3.9-4.4mm (4.11±0.16), width 1.6-1.8mm (1.71±0.08). Leg article percentages: foreleg - 7:4:23:41:8:2:3:3:9; midleg - 7:3:23:40:8:2:3:3:9; hindleg - 9:4:26:38:6:2:3:3:9. Length of t1/t5: foreleg - .74-1.0 (.85±.07); midleg - .81-1.0 (.90±.07); hindleg - .62-.75 (.69±.05).

Egg: Extracted from immature pupae - white, circular, 0.12-0.14mm diameter; from mature pupae and adults - light green, ovoid, 0.30-0.34mm in length, 0.12-0.14mm in width.

Holotype ♂ (reared from pupa): "USA, Wa. Klickitat Co., Major Creek [1.3mi above Co Rd 1230] 45°43'N 121°21'W [120m], 26.IV.85 coll. G.W. Courtney"; "reared in laboratory, emerged 1.V.85"; "crit. point dried from alcohol"; specimen on pin with head capsule, genitalia, and pupal exuviae in glycerin: deposited in USNM.

Allotype ♀ (reared from pupa): same data as holotype; specimen on pin, with pupal exuviae in glycerin; deposited in USNM.

Paratypes: **United States**; WASHINGTON, Klickitat Co.: Major Ck @ Hwy 14 Xing, 45°42'N 121°21'W 32m, 26.IV.85 (*G.W. Courtney*) [13 L, 16 P, 380 ♂, 20 ♀], 1.V.86 [12 ♂]; Major Ck @ County Rd 1230, 45°43'N 121°21'W 60m, 17.IV.83 (*G.W. Courtney*) [8 L, 22 P, 7 ♂], 21.IV.84 [2 L, 60 P, 40 ♂], 18.IV.85 [11 L, 80 P]; Major Ck [1.3mi above County Rd 1230], 45°43'N 121°21'W 120m, 21.IV.84 (*G.W. Courtney*) [4 L, 23 P, 11 ♂], 4.V.84 [4 L, 2 P], 19.IV.85 [9 L, 5 P], 26.IV.85 [12 L, 65 P, 94 ♂ (4 reared), 2 ♀ (reared)], 16.V.85 [16 P]; Yakima Co.: Satus Ck below Highbridge Spring, 46°05'N 120°32'W 480m, 7.IV.86 (*G.W. Courtney*) [5 L]. Paratypes deposited in BMNH, CNC, GWC, OrSU , USNM.

Other material examined: **United States**; WASHINGTON, Klickitat Co.: Major Ck @ Hwy 14 Xing, 45°42'N 121°21'W 32m, 20.III.86 (*G.W. Courtney*) [15 L], 27.III.86 [45 L], 2.IV.86 [56 L, 4 P], 9.IV.86 [111 L, 12 P], 17.IV.86 [50 L, 55 P], 23.IV.86 [106 L, 60 P], 1.V.86 [49 L, 38 P], 7.V.86 [20 L, 26 P], 15.V.86 [1 L, 25 P], 22.V.86 [1 P]; Major Ck @ County Rd 1230, 45°43'N 121°21'W 60m, 21.II.84 (*G.W. Courtney*) [8 L], 26.II.84 [35 L]; Major Ck [1.3mi above County Rd 1230], 45°43'N 121°21'W 120m, 26.IV.85 (*G.W. Courtney*) [35 P]. All deposited in GWC.

Derivation of specific epithet: From the Latin for occurring in Spring, in reference to the early seasonal activity of this species.

Distribution: South-central Washington (Fig. 83). Known only from: (1) Major Creek, a tributary of the Columbia River; (2) Satus Creek, a tributary of the Yakima River.

Bionomics: The type locality of *D. vernalis*, Major Creek, is a 3rd order stream at the east end of the Columbia River Gorge. The stream's lower reaches flow through a semi-exposed valley with sparse riparian vegetation (primarily *Salix* sp., *Quercus garryana* Doug., and *Pinus ponderosae* Doug.). Stream exposure contributes to relatively harsh thermal and hydrologic conditions, with winter temperatures near 0°C, periodic spring flooding, and rapidly increasing temperatures (to >30°C) and decreasing stream discharge during summer. Stream substrates consist primarily of coarse basalts. Satus Creek is a 4th order stream in a similar, but slightly more arid, setting.

Habitat features for *D. vernalis* are similar to those listed for *D. personata*. At Major Creek, *D. vernalis* coexists with the blephariceridѕ *Agathon elegantulus* von Röder, *A. sequoiarum* (Alexander), *A. comstocki*, and *Blepharicera jordani*.

Observations at Major Creek indicate that adults begin emerging at *ca*. 0800h, with the entire emergence period lasting *ca*. 30-45 minutes. Flight behaviour of *D. vernalis* is similar to that of *D. personata* and other Nearctic species. Female imagos apparently can survive several hours beyond the flight period[1], as indicated by occasional afternoon collection of live females on submerged rocks or streamside spider webs (ex. *Tetragnatha elongata* Walckenaer). Spider web collection of adult mountain midges corroborate that male *D. vernalis* are most active near the water surface. In contrast, females are rarely found in webs, presumably because individual females fly for shorter periods of time and at greater heights than males. Oviposition on submerged substrates is suggested by collection of live, wingless *D. vernalis* females from larval habitats, and by observation of females in flowing-water rearing tanks. Fecundity estimates ranged from 61 - 128 eggs / female pupa (88.7±15.8, N=36) and was correlated with pupal size (see chapter 5).

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[1] Data for other Nearctic species indicate that this may be true of all Deuterophlebiidae.

At the type locality, *D. vernalis* has a relatively brief and early activity period, with larval to adult development from mid February to early May, and the remainder of the year passed as an egg. Unlike most Nearctic species, *D. vernalis* demonstrates considerable developmental synchrony and an apparently bivoltine life history (see chapter 5).

4.5.3.13 *Deuterophlebia nielsoni* Kennedy

(Figs. 6, 17, 29, 44, 83)

Deuterophlebia nielsoni Kennedy 1958: 206.

Diagnosis. Larva identical to Sierra Nevada populations of *D. coloradensis*. Pupa similar to *D. coloradensis*, but differing in gill structure (middle filament most closely associated with anterior filament) and abdominal microsculpture (microtubercles and adjacent cuticle irregularly sculptured). Adults identical to Sierra Nevada *D. coloradensis*.

Description[1]

Larva (Fig. 6): See Kennedy (1958). Dorsal cranial color (instar IV): mostly pale, with dark, medial patch(es) posterior to level of antennal base; clypeal lobe pale. Distal antennal article pale, without digitiform microtrichia; pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (as in Fig. 2), *at* and *mt* (as in Fig. 4b) branched setiform sensilla; *pm* simple setiform sensilla (as in Fig. 10); *sbt* (meso- and metathorax) lanciform sensilla (as in Fig. 10); *ap* with two digitiform and two setiform sensilla (as in Fig. 4b). Measurements[1] (*personal observation* (*); or Kennedy 1985, *personal communication*):

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[1] Because a detailed description of *D. nielsoni* is provided elsewhere (Kennedy 1958), only a brief summary of the more salient features for species recognition (and features not discussed by Kennedy) are presented.

Instar	Sample size	Total length (mm)	Cranial width (mm)	Crochet rows	Antennal ratio*
I	6	0.4-0.6	0.14-0.18 (0.16)	1	0:2:1
II	110	0.7-1.2	0.23-0.30 (0.26)	4*	1:7:3
III	110	1.3-3.0	0.38-0.45 (0.42)	5-7	1:5:2
IV	110	3.3-5.0	0.54-0.69 (0.62)	8-13	1:2:1

Pupa (Fig. 17): See Kennedy (1958). Gill base thick, short, at least twice as wide as long; gill filaments three in number, middle filament most closely associated with anterior filament (Figs, 17, 29). Microsculpture: Meso- and metanotum irregularly set with ovoid microtubercles and associated basal microtrichia. Abdominal sutures simple, without secondary ridges; tergites with microtubercles; associated basal microtrichia long, typically extended radially to adjacent microtubercles, with microtubercles and adjacent cuticle irregularly sculptured (Fig. 44).

Adult ♂: See Kennedy (1958). Subgenal suture distinct; postgena and oral region glabrous, but few microtrichia and setiform sensilla on ventral apex of median clypeal lobe (as in Fig. 57); mental tooth acute.

Terminalia: Dorsal plate laterally concave; posterior margin slightly emarginate, medially notched, set with setiform and chaetiform sensilla. Length of gonostylus greater than length of dorsal plate or aedeagal sheath. Aedeagus internally smooth.

Adult ♀: See Kennedy (1958). Terminalia: Anterior bridge of genital fork extended posteriorly to more than half the distance to accessory gland opening.(as in Fig.

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[1] Based mostly on Convict Creek material, which, as discussed below, may include some *D. coloradensis*. Also note that measurements given in Kennedy (1958) were inaccurate (Kennedy 1985, *personal communication*); corrected values are listed in this table.

36). Cercus with length of basal article subequal to or greater than length of distal article; articles distinguishable by obvious constriction on all but medial margin (as in Fig. 71). Length of t1/t5: foreleg - .54-.64; midleg - .56-.60; hindleg - .30-.41.

Holotype ♂: USA, California, Mono Co., Convict Creek, 37°36'N 118°50'W 2195m, VII.1951 (*H.D. Kennedy*); specimen on pin; USNM Type No. 62,230.

Collection localities[1]: **United States;** CALIFORNIA, Fresno Co.: Kings R (8mi W of Piedra); Inyo Co.: Big Pine Ck (lower), 37°08'N 118°20'W 1545m; Mono Co.: Convict Ck (lower), 37°36'N 118°50'W 2195m; Green Ck, 38°08'N 119°14'W 2375m; W Walker R (nr confl Deep Ck), 38°27'N 119°27'W 1805m; Tuolumne Co.: ? River (@ Pinecrest), 38°11'N 119°59'W 1675m.

Distribution: Known only from the Sierra Nevada of California (Fig. 83).

Bionomics: Kennedy (1954, 1958) provided detailed information about the life history of *D. nielsoni* in the eastern Sierra Nevada of California. Kennedy did not recognize the presence of two species (*D. nielsoni* and *D. coloradensis*) at his Convict Creek study site, nor was he able to accurately sample instar I larvae. Both factors may have significantly influenced some of his phenological conclusions (*e.g.*, *re.* voltinism). However, with regard to other life history parameters (*e.g.*, emergence times, swarming, overwintering stage), Kennedy's observations appear to have been both insightful and accurate (*i.e.*, based on comparison with data for other deuterophlebiid species).

Remarks: Morphology of the pupal gill has demonstrated that Kennedy's (1954, 1958) Convict Creek study site contains both *D. nielsoni* and *D. coloradensis*. The gill structure of *D. nielsoni* is unique among Deuterophlebiidae, with the middle filament most closely associated with the anterior filament, and both typically sharing a common base (Fig. 29). The *D. coloradensis* gill is characteristic of other Nearctic species, with the middle filament most closely associated with the posterior filament , and often united basally (Fig. 30). Illustrations in Kennedy (1958, figs. 1-3) suggest that the same individual may demonstrate a combination of structural types; *i.e.*, with a "*nielsoni*" gill on one side and a "*coloradensis*" gill on the other. However, such variation was not evident in any examined specimens, including pupae from the type series and Kennedy's own synoptic collection. The latter contained more than 100 pupae, of which more than 90% had exclusively *nielsoni* gills, and the remainder exclusively *coloradensis* gills. Intermediates were not present.

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[1] Material examined from all localities listed.

Deuterophlebia nielsoni and *D. coloradensis* are sympatric only at Convict and Big Pine Creeks. Otherwise, allopatric distributions are typical, with *D. nielsoni* at Pinecrest, Kings River, Green Creek and West Walker River; *D. coloradensis* occurs at McGee, Laurel, Rock Creeks (all Mono Co.), and throughout western North America (see below).

4.5.3.14 *Deuterophlebia coloradensis* Pennak

(Figs. 7, 8, 19-21, 30, 38, 42, 47, 65, 66, 71, 79, 80, 84)

Deuterophlebia sp., Muttkowski, 1927: 245.

Deuterophlebia coloradensis Pennak, 1945: 1; 1951: 1.

Deuterophlebia shasta Wirth, 1951: 49.

Deuterophlebia sp., Kennedy, 1958: 202, 203; 1960: 207.

Deuterophlebia nielsoni Kennedy, 1960: 192.

Diagnosis. Larva of Sierra Nevada (California) populations indistinguishable from *D. nielsoni*; differing from other species in the pale clypeal lobe. Pupa similar to *D. nielsoni*, but differ in gill structure (middle filament most closely associated with posterior filament) and abdominal microsculpture (microtubercles and adjacent cuticle glabrous); differing from *D. vernalis* in absence of anal projection. Adults of Sierra Nevada populations indistinguishable from *D. nielsoni* ; differs from other species (*D. personata* and *D.*

vernalis) in genitalia (dorsal plate shape in male; female cercus with articles distinguishable by constrictions) or tarsal features (length of t1/t5 in female).

Description

Larva (Figs.7, 8): Dorsal color: body pale to light brown medially; prolegs pale. Dorsal cranial color (instar IV) markedly variable: mostly pale, but some populations with distinctive color patterns (*cf.* Figs.6-8); clypeal lobe pale. Distal antennal article pale, without digitiform microtrichia; pit-like sensillum on basal 1/3 of ventral branch. Chaetotaxy: *prl* (as in Fig. 2), *at* and *mt* (as in Fig. 4b) branched setiform sensilla; *pm* simple setiform sensilla (as in Fig. 10); *sbt* (meso- and metathorax) lanciform sensilla (as in Fig. 10); *ap* with two digitiform and two setiform sensilla (as in Fig. 4b). Measurements[1]:

Instar	Sample size	Total length (mm)	Cranial width (mm)	Crochet rows	Antennal ratio
I	100	0.6-1.1 (0.87±0.11)	0.12-0.18 (0.16±0.02)	1	0:2:1
II	100	0.8-1.8 (1.42±0.20)	0.22-0.28 (0.25±0.01)	4	1:8:4
III	100	1.6-3.0 (2.34±0.35)	0.36-0.44 (0.40±0.02)	5-8	1:5:2
IV	100	2.0-4.6 (3.42±0.50)	0.50-0.68 (0.60±0.04)	7-12	1:2:1

Pupa (Figs. 19-21): Male antennal sheath coiled around periphery of ventral abdomen twice, terminated near head. Gill base thick, short, *ca.* twice as wide as long; gill filaments three in number, middle filament most closely associated with posterior filament. Thoracic tubercle typically present on margin of anterolateral mesonotum, dorsad and slightly posterior to gill base; tubercle conical and, in some populations (see remarks), with apex darkly sclerotized or bearing thick, short spine (Fig. 19). Mesonotal bands transverse, raised, darkly sclerotized, between thoracic tubercle and ecdysial line. In some specimens (*e.g.*, large male pupae), mesonotum with one pair of small, raised, darkly sclerotized dots anterodorsally. Metanotal bands similar to mesonotal bands, but less darkly sclerotized and shorter. In some populations, abdominal segments I-VII each with

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[1] Based on larvae (50 of each instar) from the Clackamas and South Fork Alsea Rivers.

prominent dorsal tubercle on either side of midline (Fig. 20). Abdominal segments I, II, VI and VII laterally with *ca.* seven, ten, four and eight thorn-like spines, respectively.

Microsculpture: Meso- and metanotum irregularly set with ovoid microtubercles and associated basal microtrichia. Abdominal sutures simple, without secondary ridges; tergites with microtubercles; associated basal microtrichia long, typically extended radially to adjacent microtubercles; microtubercles and adjacent cuticle glabrous (Fig. 42).

Measurements[1]. Male pupae (N=145): Total length 2.3-3.2mm (2.76±0.15), width 1.6-2.2mm (1.91±0.10). Female pupae (N=170): Total length 2.2-2.9mm (2.49±0.14), width 1.4-2.1mm (1.77±0.12).

Adult ♂: Median clypeal lobe pronounced, broadly convex, *ca.* 25μm long, with *ca.* 25 setiform sensilla (as in Figs. 31, 52); lateral lobes pronounced, densely set with microtrichia. Anterior tentorial pits *ca.* 65μm posterior to clypeal incision. Compound eyes glabrous. Subgenal suture distinct; postgena and oral region glabrous, but few microtrichia and setiform sensilla on ventral apex of median clypeal lobe (as in Fig. 57); mental tooth acute. Antennal f1 distally with small anteroventral tubercle bearing 6-10 digitiform sensilla; f2 and f3 distally with anteroventral tubercle bearing 7-10 digitiform sensilla. Coxa, trochanter and femur with simple macrotrichia; fore and middle tibia sparsely set with simple macrotrichia, distally with abundant capitate macrotrichia, especially on ventral margin (as in Fig. 58). Hind tibia with simple macrotrichia on dorsal margin; capitate macrotrichia abundant on ventral margin, sparsely distributed on distal part of dorsal margin. All tarsi ventrally with capitate macrotrichia.

Terminalia: Dorsal plate highly variable (*cf.* Figs. 78, 80); usually laterally concave, with posterior margin slightly emarginate, medially notched, and set with setiform and chaetiform sensilla. Gonostylus longer than dorsal plate or aedeagal sheath. Aedeagus internally smooth.

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[1] Based on pupae from the South Fork Alsea River.

Measurements (N=10)[1]: Total body length 1.8-2.2mm (2.03±0.11). Antennal length 7.7-9.2mm (8.00±0.53); article length ratio 2.5:1:4:1.5:2:145. Wing length 3.4-3.9mm (3.59±0.21), width 1.5-1.8mm (1.65±0.12). Leg article percentages: foreleg - 6:5:23:36:17:4:4:3:2; midleg - 7:5:24:29:19:5:5:4:3; hindleg - 7:5:30:36:7:4:4:3:3.

Adult ♀: Similar to male. Median clypeal lobe pronounced, convex, *ca.* 30µm long, with *ca.* 20 setiform sensilla (as in Fig. 32); clypeus laterally without pronounced lobes or dense microtrichia, though microtrichia often present near subgenal suture. Anterior tentorial pits *ca.* 35µm posterior to clypeal incision. Antennal pedicel with *ca.* 3-5 setiform sensilla; f1-4 narrow basally, expanded distally; each of f1-3 distally with anteroventral prominence bearing 2-3 digitiform sensilla; f4 with 2-4 setiform sensilla, and, anteroventrally, 3-5 digitiform sensilla.

Terminalia: Anterior bridge of genital fork posteriorly acute, extended more than half the distance to accessory gland opening.(as in Fig. 36). Cercus with length of basal article subequal to or greater than length of distal article; articles distinguishable by obvious constriction on all but medial margin (Fig. 71).

Measurements (N=10)[2]: Total body length 1.5-2.0mm (1.65±0.16). Antennal length 0.29-0.37mm (0.33±0.03); article length ratio 2:1:2.5:1:1:1. Wing length 3.0-3.9mm (3.34±0.35), width 1.2-1.6mm (1.36±0.13). Leg article percentages: foreleg - 7:4:25:39:7:2:3:3:11; midleg - 7:4:25:38:6:2:3:3:11; hindleg - 10:4:27:38:4:2:3:3:11. Length of t1/t5: foreleg - .56-.73 (.62±.06); midleg - .52-.67 (.58±.05); hindleg - .33-.45 (.38±.04).

Egg: Extracted from immature pupae - white, circular, 0.12-0.14mm diameter; from mature pupae or adults - light green, ovoid, 0.30-0.34mm in length, 0.12-0.14mm in width.

Holotype: See below.

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[1] Based on males from Middle Fork Boulder Creek, Colorado.

[2] Based on females from Colorado (East River and Middle Fork Boulder Creek).

Lectotype Designation: In his original description of *D. coloradensis*, Pennak (1945) designated a "Holotype mature larva" (pg. 4) and "Holotype female pupa" (pg. 6). This contravenes the International Code of Zoological Nomenclature, which specifies [Article 73] that only a **single** specimen may be designated holotype. Thus, the *D. coloradensis* "holotype" larva and pupa carry equal status as syntypes (*sensu* ICZN). I hereby designate as lectotype the female pupa; the specimen is mounted on a slide and carries the following handwritten labels: "Boulder Creek; Boulder Co., Colo.; Altitude 1810m; July 31, 1944; R.W. PENNAK, coll"; "DEUTEROPHLEBIIDAE; *Deuterophlebia coloradensis*; Mature ♀ pupa Holotype". To these labels I have added [across bottom of slide] the label "LECTOTYPE; designated by G.W. Courtney 1989". The larval specimen [a ♂], slide-mounted and labelled: "Boulder Creek; Boulder Co., Colo.; Altitude 1810m; July 31, 1944; R.W. PENNAK, coll"; "DEUTEROPHLEBIIDAE; *Deuterophlebia coloradensis*; Mature larva Holotype", is hereby designated a paralectotype, and labelled [across bottom of slide] "PARALECTOTYPE; designated by G.W. Courtney 1989". Both specimens are deposited in the AMNH.

Collection localities[1]: **Canada**; ALBERTA: Trans-Canada Hwy: Pipestone R (Banff NP), 51°25'N 116°10'W 1540m; Yellowhead Hwy: Snaring R (nr Snaring R C.G., Jasper NP), 53°00'N 118°05'W 1010m; BRITISH COLUMBIA: Trans-Canada Hwy: Emory Ck (N of Hope), 49°30'N 121°25'W 60m; Deadman Ck (W of Kamloops), 50°45'N 120°54'W 380m; Eagle R (nr Kay Falls), 50°58'N 118°36'W 420m; Yellowhead Hwy: Fraser R (ca 1km above Overlander Falls), 53°01'N 119°11'W 870m; Slim Ck (@ Hwy Xing), 53°44'N 121°09'W 710m; Hwy 5 Blue R (just below Hwy Xing), 52°07'N 119°18'W 675m; Louis Ck (S of Barriere), 51°08'N 120°07'W 380m; Cassiar Hwy: Tanzilla R (km 495), 58°22'N 129°54'W 900m; Bass Ck (km 596), 59°07'N 129°49'W 790m; Silverhope Creek Rd: Silverhope Ck (*ca.* 5km S of Hope), 49°20'N 121°27'W 185m; Silverhope Ck (@ km 15), 49°16'N 121°23'W 365m; Alaska Hwy: Tributary,

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[1] Material examined from most localities listed.

Trout R (km 766), 59°12'N 125°56'W 690m; Crowsnest Hwy: Similkameen R (ca 1km above Copper Ck), 49°11'N 120°33'W 935m; Similkameen R (nr Muledeer Provincial Park), 49°04'N 120°41'W 1080m; YUKON: Alaska Hwy: Little Rancheria R (km 1079), 60°08'N 129°36'W 755m; Big Ck (km 1084), 60°09'N 129°42'W 775m; Spencer Ck (km 1119), 60°08'N 130°13'W 860m; Upper Rancheria R (km 1162), 60°04'N 130°55'W 975m; Seagull Ck (km 1180), 60°00'N 131°11'W 890m; Wolf Ck (km 1458), 60°36'N 134°56'W 715m; Klondike Loop: Klondike R (23.5km E of Dawson), 64°03'N 139°03'W 385m; Klondike R (17km E of Dawson), 64°02'N 139°07'W 380m; Campbell Hwy: Tuchitua R (km 108.5), 60°55'N 129°13'W 730m; Money Ck (km 168), 61°24'N 129°39'W 680m; Big Campbell Ck (km 262.5), 61°45'N 131°07'W 840m; Hoole R (km 297.5), 61°44'N 131°42'W 810m; Starr Ck (km 306.5), 61°46'N 131°51'W 840m; Lapie R (@ Lapie R Canyon, km 360), 61°59'N 132°35'W 730m; Truitt Ck (ca km 460), 62°12'N 134°22'W 625m; Drury Ck (km 460.5), 62°12'N 134°23'W 615m; Bearfeed Ck (km 498), 62°11'N 135°04'W 625m; Little Salmon R (ca km 554), 62°05'N 135°34'W 550m; Dempster Hwy: E Fk Blackstone R (km 113), 64°47'N 138°21'W 1010m; Blackstone R (km 141), 64°57'N 138°14'W 910m; Ogilvie R (ca km 200), 65°22'N 138°18'W 600m; South Canol Rd: Rose R (km 150), 61°32'N 133°05'W 1020m; Upper Sheep Ck (@ Hwy Xing, km 156), 61°33'N 133°05'W 1065m; Pony Ck (km 160), 61°35'N 133°05'W 1090m; Nahanni Range Rd: Dolly Varden Ck (km 39.5), 60°57'N 127°37'W 850m;? Hyland R (km 111.5), 61°29'N 128°13'W 850m; Hyland R (ca km 152), 61°48'N 128°17'W 1100m; **United States**; ALASKA: Champion Ck (N of Chicken), 64°33'N 142°08'W 600m; CALIFORNIA, Humboldt Co.: Bluff Ck (nr confl Klamath R), 41°14'N 123°39'W 120m; Van Duzen R (@ Bridgeville), 40°28'N 123°47'W 195m; Inyo Co.: Big Pine Ck (lower), 37°08'N 118°20'W 1545m; Big Pine Ck (@ Sage Flat), 37°07'N 118°23'W 2075m; Madera Co.: Minaret Ck (below Falls), 37°38'N 119°05'W 2310m; Mendicino Co.: M Fk Eel R (nr Dos Rios), 39°42'N 123°20'W 275m; M Fk Eel R (1.3mi above confl Williams Ck), 39°49'N 123°06'W 440m; Mono Co.:

Convict Ck (lower), 37°36'N 118°50'W 2195m; Convict Ck (nr confl Genevieve Ck), 37°33'N 118°52'W 2745m; Laurel Ck (nr trailhead), 37°35'N 118°55'W 2745m; Little Walker R, 38°18'N 119°27'W 2225m; McGee Ck (@ trailhead), 37°32'N 118°49'W 2515m; Rock Ck (@ lower Xing), 37°32'N 118°41'W 2285m; Rock Ck (@ E Fk Xing), 37°29'N 118°43'W 2700m; Siskiyou Co.: Indian Ck (ca 7mi N of Happy Camp), 41°55'N 123°28'W 560m; Scott R (@ 1km above confl Klamath R), 41°46'N 123°01'W 470m; Tehama Co.: Thomes Ck (ca 1mi below Paskenta), 39°53'N 122°31'W 215m; Trinity Co.: N Fk Trinity R, 40°47'N 123°07'W 420m; Trinity R (5.3mi below Del Loma), 40°47'N 123°24'W 305m; COLORADO, Archuleta Co.: E Fk San Juan R (@ C.G.), 37°22'N 106°52'W 2340m; Navajo R (above Price Lakes turnoff), 37°03'N 106°41'W 2395m; Piedra R (1mi above Chimney Rock), 37°14'N 107°20'W 2000m; Turkey Ck (@ Hwy 160 Xing), 37°21'N 106°55'W 2285m; Rio Blanco (0.5mi above Hwy 84), 37°08'N 106°54'W 2165m; Rio Blanco (upper), 37°14'N 106°45'W 2485m; Boulder Co.: Boulder Ck (@ Boulder), 40°00'N 105°15'W 1680m; Boulder Ck (ca 1mi below Sugarloaf Rd), 40°00'N 105°20'W 1815m; Boulder Ck (upper, approx), 40°00'N 105°24'W 2100m; M Fk Boulder Ck (1.5mi below Barker Res), 39°58'N 105°27'W 2395m; N Boulder Ck (nr Gordon Gulch ?), 40°00'N 105°24'W 2190m; N Boulder Ck (upper, approx), 39°59'N 105°32'W 2750m; N St. Vrain Ck (NW of Lyons), 40°13'N 105°16'W 1645m; S St. Vrain Ck (ca 4mi SW of Lyons), 40°12'N 105°19'W 1715m; St. Vrain Ck (@ Lyons), 40°13'N 105°15'W 1690m; Chaffee Co.: Chalk Ck (@ Nathrop), 38°44'N 106°05'W 2340m; S Arkansas R (ca 1mi above Maysville), 38°32'N 106°12'W 2545m; Clear Creek Co.: Fall R (nr confl Clear Ck), 39°45'N 105°33'W 2355m; Conejos Co.:Alamosa R (NW of Capulin), 37°18'N 106°08'W 2420m; Gunnison Co.: Beaver Ck (nr confl Blue Mesa Res), 38°29'N 107°01'W 2300m; Cement Ck (nr C.G.), 38°49'N 106°49'W 2760m; East R (nr Roaring Judy Fish Hatchery), 38°42'N 106°51'W 2480m; East R (nr confl Cement Ck), 38°48'N 106°53'W 2600m; Gunnison R (@ Hwy 135 Xing), 38°34'N 106°55'W 2365m; Gunnison R (@ Almont C.G.), 38°39'N 106°51'W 2430m; Lake Fk Gunnison R

(@ "The Gate"), 38°14'N 107°15'W 2430m; Taylor R (ca 3.5mi above Almont), 38°41'N 106°48'W; Hinsdale Co.: N Fk Clear Ck (@ Hwy 149 Xing), 37°51'N 107°09'W 3055m; Jackson Co.: S Fk Michigan R (nr Gould), 40°33'N 106°02'W 2665m; Lake Co.: Lake Ck (@ Parry Peak C.G.), 39°04'N 106°24'W 2865m; La Plata Co.: Hermosa Ck (@ Hermosa), 37°24'N 107°50'W 2025m; Larimer Co.: Big Thompson R (W of Loveland), 40°25'N 105°10'W 1550m; Big Thompson R (@ Narrows Rest Area), 40°24'N 105°15'W 1690m; Big Thompson R (above Estes Park), 40°22'N 105°40'W 2750m; Cache la Poudre R (ca 1.5mi below Boyd Gulch), 40°42'N 105°14'W 1640m; Cache la Poudre R (@ Narrows Picnic Area), 40°41'N 105°25'W 1965m; Cache la Poudre R (nr Tunnel Picnic Area), 40°40'N 105°48'W 2435m; Mineral Co.: Clear Ck (@ Hwy 149 Xing), 37°46'N 107°06'W 2745m; Rio Grande (@ Marshall Park), 37°47'N 106°59'W 2650m; Wolf Ck (nr C.G.), 37°26'N 106°53'W 2375m; Montrose Co.: Gunnison R (in Canyon, approx), 38°31'N 107°39'W 1980m; Rio Grande Co.: Beaver Ck (nr "Upper" C.G.), 37°36'N 106°40'W 2580m; S Fk Rio Grande (@ F.S. Rd 360 Xing), 37°39'N 106°39'W 2515m; Saguache Co.:Tomichi Ck (@ Picnic Area), 38°23'N 106°26'W 2550m; IDAHO, Adams Co.: Little Salmon R (nr Elk Lk Rd), 45°12'N 116°18'W 900m; Boise Co.: Boise R (nr confl Willow Ck), 43°39'N 115°46'W 935m; Canyon Ck (ca 5mi above S Fk Payette R), 44°13'N 115°13'W 1755m; Clear Ck (@ Lowman), 44°05'N 115°36'W 1165m; Deadwood R (@ C.G.), 44°04'N 115°39'W 1120m; Deadwood R (nr confl Slaughterhouse Ck), 44°06'N 115°39'W 1160m; N Fk Boise R (nr confl Bear R), 43°53'N 115°29'W 1370m; N Fk Boise R (@ F.S. Rd 327 Xing), 43°54'N 115°24'W 1470m; Payette R (2.5mi above confl N Fk), 44°05'N 116°04'W 880m; S Fk Payette R (@ Pine Flats), 44°03'N 115°40'W 1090m; S Fk Payette R (nr confl Canyon Ck), 44°10'N 115°14'W 1465m; Bonner Co.: Hughes Fk (@ F.S. Rd 1013 Xing), 48°49'N 116°58'W 825m; Custer Co.: E Fk Salmon R (ca 0.5mi above confl Road Ck), 44°10'N 114°17'W 1720m; Marsh Ck (@ Lola Ck C.G.), 44°24'N 115°10'W 1965m; Salmon R (nr confl Slate Ck), 44°15'N 114°33'W 1720m; Salmon R (ca 0.5mi below Stanley), 44°13'N 114°55'W 1890m; Slate Ck (nr confl Salmon R), 44°15'N 114°33'W 1720m; Yankee Fk (nr confl Blind Ck), 44°17'N 114°43'W 1830m; Elmore Co.: Boise R (1mi below confl N & M Fk's), 43°42'N 115°38'W 1020m; M Fk Boise R (nr confl Pete Ck), 43°44'N 115°36'W 1065m; M Fk Boise R (nr confl Granite Ck), 43°48'N 115°24'W 1280m; M Fk Boise R (nr confl Steppe Ck), 43°49'N 115°17'W 1380m; M Fk Boise R (nr confl Fall Ck), 43°48'N 115°11'W 1510m; Queens R (nr confl China Fk Ck), 43°49'N 115°12'W 1515m; Yuba R (@ F.S. Rd 268 Xing), 43°48'N 115°09'W 1580m; Fremont Co.: Falls R (@ County Rd 261 Xing), 44°03'N 111°21'W 1615m; Warm R (nr confl Robinson Ck), 44°06'N 111°19'W 1610m; Idaho Co.: Crooked Fk (ca 3mi below Hwy 12 Xing), 46°33'N 114°39'W 1115m; Fish Ck (nr confl Lochsa R), 46°20'N 115°20'W 610m; Rapid R (@ trailhead), 45°21'N 116°23'W 665m; S Fk Clearwater R (ca 1mi below Castle Ck), 45°49'N 115°58'W 685m; Latah Co.: Little Boulder Ck (nr confl Potlatch R), 46°46'N 116°26'W 800m; Potlatch R (ca 3mi S of Helmer), 46°46'N 116°26'W 800m; Lemhi Co.: Cow Ck (nr confl Salmon R), 44°44'N 114°00'W 1410m; N Fk Salmon R (nr confl Sheep Ck), 45°30'N 113°56'W 1280m; Teton Co.: Bitch Ck (@ Hwy 32 Xing), 43°56'N 111°10'W 1785m; Valley Co.: Indian Ck (nr confl M Fk Salmon R), 44°46'N 115°06'W 1415m; N Fk Payette R (@ Big Eddy C.G.), 44°13'N 116°06'W 1235m; N Fk Payette R (nr confl Round Valley Ck), 44°19'N 116°03'W 1395m; MONTANA, Flathead Co.: Avalanche Ck (Glacier NP), 48°39'N 113°47'W 1190m; Bear Ck (nr confl M Fk Flathead R), 48°14'N 113°34'W 1180m; Bear Ck (ca 4mi below Marias Pass), 48°17'N 113°25'W 1375m; Big Ck (@ F.S. Rd 830 Xing), 48°35'N 114°13'W 1075m; Bowman Ck (@ C.G., Glacier NP), 48°47'N 114°16'W 1080m; Hay Ck (@ F.S. Rd 376 Xing), 48°46'N 114°20'W 1220m; Kintla Ck (@ Route 7 Xing, Glacier NP), 48°55'N 114°22'W 1170m; Lincoln/Walton Ck's (Glacier NP), 48°33'N 113°51'W 1160m; M Fk Flathead R (nr confl Paola Ck), 48°20'N 113°38'W 1095m; Quartz Ck (nr C.G., Glacier NP), 48°43'N 114°13'W 1075m; Red Meadow Ck (@ F.S. Rd 210 Xing), 48°48'N 114°21'W 1145m; Stanton Ck (nr Hwy 2 Xing), 48°23'N 113°42'W 1090m; Whale Ck (@ F.S. Rd

210 Xing), 48°51'N 114°21'W 1130m; Gallatin Co.: Gallatin R (@ Sheds Bridge), 45°40'N 111°12'W 1425m; Gallatin R (nr confl Spanish Ck), 45°29'N 111°16'W 1580m; Gallatin R (@ Jack Smith Bridge), 45°16'N 111°13'W 1800m; Gallatin R (@ Almart), 45°07'N 111°13'W 1950m; Gallatin R (nr confl Sage Ck), 45°04'N 111°11'W 2010m; Hellroaring Ck, 45°26'N 111°14'W 1645m; Hyalite Ck (in Canyon, approx), 45°33'N 111°03'W 1735m; N/M Fk Gallatin R (nr confl), 45°15'N 111°19'W 1920m; Spanish Ck (nr confl Gallatin R), 45°29'N 111°16'W 1580m; Specimen Ck (nr confl Gallatin R), 45°00'N 111°04'W 2120m; Glacier Co.: Divide Ck (@ St Mary), 48°44'N 113°25'W 1400m; Kennedy Ck (@ Hwy 89 Xing), 48°55'N 113°26'W 1370m; Lee Ck (@ Hwy 17 Xing), 48°59'N 113°37'W 1585m; Two Medicine R (@ Hwy 49 Xing), 48°28'N 113°14'W 1435m; Lewis & Clark Co.: Dearborn R (nr confl Missouri R), 47°07'N 111°54'W 1045m; Madison Co.: Madison R (below W Fk Madison R), 44°53'N 111°35'W 1785m; Yellowstone NP Co.: Grayling Ck (@ Hwy 191 Xing), 44°51'N 111°03'W 2100m; Madison R (nr West Entrance), 44°39'N 111°03'W 2020m; NEW MEXICO, Rio Arriba Co.: M Fk Rio Santa Barbara, 36°00'N 105°35'W 2440m; Rio Chama (@ Chama), 36°52'N 106°35'W 2360m; Embudo Ck (nr confl Rio Grande), 36°12'N 105°54'W 1785m; Rio Vallecitos (nr confl Rock Ck, El Vallecito); Rio Tusas (nr Las Tablas), 36°33'N 106°02'W 2290m; San Miguel Co.: Pecos R (@ Dalton Rest Area), 35°39'N 105°41'W 2190m; Santa Fe Co.: Rio Frijoles (nr Cundiyo), 35°57'N 105°54'W 1980m; OREGON, Baker Co.: N Fk Powder R (below Rocky Ford C.G.), 44°59'N 118°04'W 1145m; Benton Co.: Crooked Ck (nr confl Ernest Ck), 44°25'N 123°32'W 130m; Crooked Ck (nr confl Cabin Ck), 44°26'N 123°31'W 160m; Greasy Ck (5mi W of Philomath), 44°30'N 123°26'W 105m; Marys R (@ Hwy 20 Xing, NW of Philomath), 44°32'N 123°24'W 85m; Marys R (@ Hwy 223 Xing, N of Wren), 44°35'N 123°25'W 130m; N Fk Alsea River (@ Hwy 34 Xing), 44°24'N 123°33'W 105m; Rock Ck (@ Hwy 34 Xing), 44°30'N 123°26'W 120m; Rock Ck (middle), 44°30'N 123°26'W 130m; Rock Ck (upper), 44°30'N 123°27'W 135m; S Fk Alsea R (ca 2mi up S Fk Rd), 44°21'N

123°34'W 105m; S Fk Alsea R (@ S Fk Rd Xing), 44°20'N 123°32'W 180m; Willamette R ? (N of Peoria Slough), 44°30'N 123°12'W 67m; Woods Ck (0.5mi up Woods Ck Rd), 44°33'N 123°25'W 105m; Clackamas Co.: Clackamas R (nr confl Moore Ck), 45°11'N 122°10'W 230m; Clackamas R (below confl Roaring R), 45°09'N 122°07'W 290m; Clackamas R (nr confl Roaring R), 45°09'N 122°06'W 295m; Clackamas R (above Three Lynx), 45°07'N 122°04'W 340m; Clackamas R (nr confl Collawash R), 45°01'N 122°03'W 445m; Clackamas R (nr Austin Hot Springs), 45°01'N 122°00'W 500m; Clear Ck (@ FS Rd 1820 Xing), 45°23'N 121°54'W 550m; Collawash R (ca 2mi above confl Clackamas R), 45°01'N 122°03'W 455m; Hot Springs Ck (above F.S. Rd 63 Xing), 44°59'N 122°04'W 505m; Molalla R (above Hwy 211 Xing), 45°09'N 122°32'W 90m; Oak Grove Fk Clackamas R (@ C.G.), 45°04'N 122°02'W 440m; Roaring R (above C.G.), 45°09'N 122°06'W 295m; S Fk Salmon R (nr confl Salmon R), 45°16'N 121°56'W 500m; Columbia Co.: Clatskanie R (@ Swedetown Rd Xing), 46°02'N 123°07'W 73m; Clatskanie R (nr confl Little Clatskanie R), 45°59'N 123°02'W 185m; Coos Co.: Rock Ck (@ C.G.), 42°42'N 124°03'W 350m; S Fk Coquille R (nr confl Coal Ck), 42°49'N 124°00'W 120m; S Fk Coquille R (ca 1mi above confl Elk Ck), 42°48'N 124°01'W 145m; S Fk Coquille R (@ Daphne Grove), 42°44'N 124°03'W 250m; Curry Co.: Illinois R (@ Oak Flat), 42°30'N 124°02'W 46m; Lawson Ck (@ Oak Flat), 42°30'N 124°02'W 46m; Douglas Co.: Boulder Ck (1mi above confl S Umpqua R), 43°03'N 122°46'W 440m; Drew Ck (nr confl Elk Ck), 42°53'N 122°55'W 390m; Dumont Ck (nr confl S Umpqua R), 43°02'N 122°48'W 410m; Dumont Ck (middle), 43°02'N 122°48'W 425m; Dumont Ck (upper), 43°03'N 122°49'W 450m; Elk Ck (2.9mi SE of Tiller), 42°53'N 122°55'W 375m; Elk Ck (nr confl Drew Ck), 42°53'N 122°55'W 390m; Jackson Ck (nr confl Beaver Ck), 42°57'N 122°49'W 395m; N Umpqua R (ca 4mi below Steamboat), 43°19'N 122°47'W 315m; Quines Ck (@ Quines Ck), 42°46'N 123°16'W 475m; Rock Ck (nr confl N Umpqua R), 43°20'N 123°00'W 230m; Smith R (1.6mi below confl Vincent Ck), 43°48'N 123°48'W 43m; S Umpqua R (@ Winston), 43°06'N

123°23'W 145m; S Umpqua R (@ Myrtle Ck), 43°01'N 123°18'W 185m; S Umpqua R (2.3mi W of Tiller), 42°57'N 122°59'W 285m; S Umpqua R (6.8mi NE of Tiller), 42°59'N 122°52'W 350m; S Umpqua R (nr confl Dumont Ck), 43°02'N 122°48'W 410m; S Umpqua R (ca 2mi above S Ump Falls), 43°04'N 122°39'W 535m; Steamboat Ck (nr confl Canton Ck), 43°21'N 122°43'W 350m; Steamboat Ck (@ F.S. Rd 38 Xing), 43°24'N 122°36'W 480m; W Fk Smith R (2.2mi above confl Smith R), 43°49'N 123°45'W 78m; Grant Co.: M Fk John Day R (@ Hwy 395 Xing), 44°50'N 119°01'W 885m; Jackson Co.: Elk Ck (ca 1mi above confl Rogue R), 42°40'N 122°44'W 455m; Jefferson Co.: Metolius R (ca 1mi above Monty C.G), 44°38'N 121°30'W 620m; Josephine Co.: Grave Ck (@ I-5 Xing), 42°38'N 123°23'W 325m; Illinois R (@ Eight Dollar Mt. Rd Xing), 42°14'N 123°41'W 350m; Lane Co.: Blue R (@ F.S. Rd 15 Xing), 44°13'N 122°15'W 425m; Blue R (nr confl Cook Ck), 44°15'N 122°13'W 505m; Deer Ck (ca 1mi above confl McKenzie R), 44°15'N 122°03'W 580m; Greenleaf Ck (@ Hwy 36 Xing), 44°07'N 123°37'W 115m; Hills Ck (ca 2mi above Hills Ck Res), 43°40'N 122°22'N, 495m; Horse Ck (ca 1mi above Foley Springs), 44°09'N 122°04'N 550m; Lake Ck (3.5mi below confl Greenleaf Ck), 44°06'N 123°40'W 100m; Lookout Ck (@ H.J. Andrews Adm. Site), 44°12'N 122°15'W 425m; McKenzie R (above confl S Fk McKenzie R), 44°09'N 122°16'W 340m; McKenzie R (nr confl Deer Ck), 44°14'N 122°03'W 560m; M Fk Willamette R (@ Sand Prairie), 43°36'N 122°27'W 475m; M Fk Willamette R (@ F.S. Rd 2127 Xing), 43°32'N 122°26'W 545m; N Fk Willamette R (4.1mi above Westfir), 43°47'N 122°26'W 355m; N Fk Willamette R (@ Kiahanie), 43°53'N 122°16'W 645m; Salmon Ck (above Oakridge), 43°44'N 122°25'W 385m; Salt Ck (@ F.S. Rd 5875 Xing), 43°42'N 122°16'W 610m; Siuslaw R (nr confl Whittaker Ck), 43°59'N 123°39'W 85m; S Fk McKenzie R (@ F.S. Rd 1980 Xing), 44°01'N 122°12'W 540m; S Fk McKenzie R (nr confl Trail Ck), 44°00'N 122°10'W 620m; Wildcat Ck (ca 1mi above confl Siuslaw R), 44°00'N 123°38'W 100m; Wolf Ck (nr confl Siuslaw R), 43°57'N 123°37'W 105m; Lincoln Co.: Siletz R (below Twin Bridges/Sam Ck

Bridge), 44°44'N 123°50'W 40m; Siletz R (@ Moonshine Park), 44°46'N 123°49'W 70m; Siletz R (nr confl Sunshine Ck), 44°49'N 123°46'W 135m; Linn Co.: Calapooia R (nr confl Bigs Ck), 44°17'N 122°37'W 275m; Marion Ck (above Hwy 22 Xing), 44°36'N 121°57'W 745m; N Santiam R (nr confl Pamelia Ck), 44°39'N 121°57'W 655m; N Santiam R (3.9mi below Hwy 22 Xing), 44°33'N 121°59'W 885m; S Santiam R (@ Hwy 20 Xing), 44°23'N 122°23'W 320m; Thomas Ck (ca 10mi above Scio), 44°42'N 122°33'W 245m; Wiley Ck (nr confl Little Wiley Ck), 44°22'N 122°37'W 225m; Marion Co.: Breitenbush R (@ Cleator Bend), 44°46'N 121°59'W 640m; N Santiam R (ca 0.5mi above Detroit Res), 44°42'N 122°05'W 490m; N Santiam R (@ Whispering Falls), 44°41'N 122°00'W 600m; Polk Co.: Little Luckiamute R (@ Falls City), 44°52'N 123°26'W 105m; Mill Ck (nr Buell), 45°01'N 123°25'W 110m; Rickreall Ck (@ Dallas), 44°55'N 123°19'W 90m; Tillamook Co.: Nestucca R (@ Beaver), 45°16'N 123°48'W 23m; Nestucca R (3.3mi above Blaine), 45°15'N 123°39'W 115m; Nestucca R (@ Alder Glen C.G.), 45°16'N 123°34'W 220m; Salmonberry R (nr confl Nehalem R), 45°45'N 123°39'W 61m; Three Rivers (nr Hebo), 45°13'N 123°51'W 12m; Three Rivers (nr confl Cedar Ck), 45°12'N 123°50'W 23m; Trask R (@ "The Peninsula"), 45°27'N 123°40'W 46m; Wilson R (@ Keenig C.G.), 45°32'N 123°36'W 98m; Wilson R (@ nr confl Ben Smith Ck), 45°35'N 123°31'W 185m; Umatilla Co.: N Fk John Day R (@ Hwy 395 Xing), 44°50'N 119°01'W 885m; Union Co.: Grande Ronde R (@ Red Bridge), 45°17'N 118°19'W 960m; Wallowa Co.: Imnaha R (@ Imnaha), 45°33'N 116°49'W 600m; Little Sheep Ck (approx), 45°26'N 117°00'W 1005m; Minam R (nr confl Wallowa R), 45°37'N 117°43'W 775m; Yamhill Co.: Coast Ck (nr confl Willamina Ck), 45°09'N 123°29'W 105m; Willamina Ck (5.8mi above Willamina), 45°08'N 123°29'W 100m; UTAH, Beaver Co.: Beaver R (approx), 38°15'N 112°30'W 2120m; Duchesne Co.: Duchesne R (nr confl W Fk Duchesne R), 40°27'N 110°49'W 2120m; Lake Fk R (@ F.S. Rd 119 Xing), 40°28'N 110°22'W 2175m; Uinta R (@ Uinta Canyon C.G.), 40°37'N 110°08'W 2315m; Yellowstone R (@ Bridge C.G.), 40°32'N 110°20'W 2330m; Yellowstone R (@ Swift Ck

C.G.), 40°36'N 110°20'W 2455m; Summit Co.: Bear R (nr confl E Fk Bear R), 40°54'N 110°49'W 2525m; Uintah Co.: Ashley Ck (nr Rock Canyon), 40°33'N 109°37'W 1860m; Wasatch Co.: Provo R (@ Soapstone Xing), 40°34'N 111°02'W 2360m; WASHINGTON, Asotin Co.: Grande Ronde R (@ Hwy 129 Xing), 46°02'N 117°15'W 380m; Chelan Co.: Wenatchee R (@ Dryden), 47°32'N 120°34'W 290m; Wenatchee R (from HDK), 47°35'N 120°40'W 355m; Clallam Co.: Dungeness R (ca 1mi below fish hatchery), 48°02'N 123°08'W 130m; Elwha R (nr confl Madison Ck), 48°02'N 123°35'W 73m; Soleduck R (@ Hwy 101 Xing), 48°04'N 124°05'W 240m; Clark Co.: Washougal R (@ NE Vernon Rd Xing), 45°37'N 121°16'W 61m; Cowlitz Co.: Kalama R (ca 3mi above fish hatchery), 46°00'N 122°43'W 67m; Grays Harbor Co.: Quinalt R (ca 3mi above Lake Quinalt), 47°30'N 123°47'W 70m; Jefferson Co.: Big Quilcene R (@ Hwy 101 Xing), 47°48'N 122°54'W 34m; Dosewallips R (@ Hwy 101 Xing), 47°41'N 122°53'W <3 m; Dosewallips R (nr confl Rocky Brook), 47°42'N 122°56'W 30m; Dosewallips R (nr confl Tumbling Ck), 47°44'N 123°09'W 455m; Duckabush R (@ F.S. Rd 28 Xing), 47°41'N 123°02'W 99m; Hoh R (nr Minnie Peterson C.G.), 47°49'N 124°10'W 75m; N Fk Quinalt R (@ N Fk C.G.), 47°34'N 123°38'W 150m; Queets R (ca 1mi above confl Matheny Ck), 47°35'N 124°06'W 52m; King Co.: Rex R (2.3mi above Chester Morse Lk), 47°21'N 121°40'W 490m; S Fk Snoqualmie R (@ North Bend), 47°29'N 121°47'W 130m; Skykomish R (nr confl Anderson Ck), 47°49'N 121°35'W 130m; Klickitat Co.: Cispus R (nr confl Yellowjacket Ck), 46°26'N 121°50'W 385m; Yellowjacket Ck (nr confl Cispus R), 46°26'N 121°50'W 385m; Mason Co.: Hamma Hamma R (nr C.G.), 47°35'N 123°07'W 170m; Pend Oreille Co.: Sullivan Ck (nr Metaline Falls), 48°51'N 117°21'W 630m; Sullivan Ck (nr Sullivan Lk turnoff), 48°50'N 117°17'W 780m; Skagit Co.: Bacon Ck (ca 1mi above confl Skagit R), 48°36'N 121°23'W 120m; Bacon Ck (nr confl East Fk), 48°39'N 121°25'W 245m; Cascade R (nr confl Boulder Ck), 48°31'N 121°21'W 130m; Marble Ck (ca 0.5mi above confl Cascade R), 48°32'N 121°16'W 330m; Sauk R (ca 1.5mi above confl White Ck), 48°22'N 121°33'W 100m; Skamania Co.: Lewis R (@ F.S. Rd

9039 Xing), 46°03'N 121°57'W 340m; Panther Ck (@ F.S. Rd 6808 Xing), 45°46'N 121°50'W 170m; Wind R (ca 1km above confl Trapper Ck), 45°52'N 121°58'W 335m; Snohomish Co.: Elliot Ck (nr confl S Fk Sauk R), 48°04'N 121°24'W 520m; N Fk Sauk R (@ F.S. Rd 20 Xing), 48°05'N 121°23'W 370m; N Fk Stillaguamish R (@ Oso Xing), 48°16'N 122°00'W 38m; S Fk Sauk R (@ Chokowich C.G.), 48°04'N 121°23'W 425m; S Fk Stillaguamish R (nr confl Schweitzer Ck), 48°04'N 121°41'W 365m; White Chuck R (@ Crystal Springs Xing), 48°10'N 121°21'W 455m; Wahkiakum Co.: Elochoman R (@ Hwy 407 Xing), 46°13'N 123°21'W 23m; Elochoman R (@ mi 4.7, Hwy 407), 46°15'N 123°18'W 37m; Elochoman R (@ salmon hatchery), 46°16'N 123°16'W 61m; Whatcom Co.: Goodell Ck (@ Newhalem), 48°40'N 121°15'W 145m; Panther Ck (nr confl Ruby Ck), 48°42'N 120°58'W 505m; Ruby Ck (nr confl Panther Ck), 48°42'N 120°58'W 505m; Yakima Co.: Bumping R (@ Cedar Springs C.G.), 46°58'N 121°09'W 840m; Naches R (ca 6mi below Niles Rd), 46°46'N 120°50'W 520m; Naches R (@ Hwy 140 Xing), 46°59'N 121°05'W 775m; Tieton R (@ lower Hwy 12 Xing), 46°41'N 120°55'W 625m; Tieton R (@ Wild Rose C.G.), 46°40'N 121°02'W 745m; WYOMING, Fremont Co.: Wind R (10mi E of Dubois), 43°27'N 109°28'W 1965m; Johnson Co.: South Fk R ? (@ S Fk C.G.), 44°16'N 106°56'W 2325m; Lincoln Co.: Greys R (@ Bridge C.G.), 43°08'N 110°58'W 1735m; Greys R (nr confl Squaw Ck), 43°08'N 110°56'W 1775m; Greys R (nr confl Little Greys R), 43°08'N 110°52'W 1815m; Blackrock Ck (@ Hwy 26 Xing), 43°49'N 110°20'W 2095m; Teton Co.: Hoback R (ca 2mi above confl Snake R), 43°18'N 110°41'W 1815m; Clear Ck (from HDK), 44°40'N 110°50'W 2285m; Yellowstone NP Co.: Gibbon R (approx), 44°39'N 110°46'W 2135m; Lost Ck (nr Camp Roosevelt), 44°54'N 110°25'W 1920m; Tower Ck (above Falls), 44°52'N 110°22'W 2040m; Yellowstone R (@ Cooke City Bridge), 44°55'N 110°24'W 1800m.

Distribution: Widespread western Nearctic, from the Sierra Nevada of California and southern Rocky Mountains (New Mexico) to the Mackenzie Mountains (central Yukon) and extreme eastern Alaska (Fig. 84). This deuterophlebiid, and others, are noticeably absent from the Alaskan interior (*e.g.*, Alaska Range) and south coast (*e.g.*, Chugach Range). A published record from the Brooks Range (Slack *et al.* 1979) represents a misidentified *Dicranota* (Tipulidae) larva (Slack 1983, *personal communication*).

Bionomics: *Deuterophlebia coloradensis* inhabits a diversity of stream types, ranging from small, closed-canopy, mountain streams to large, exposed, lowland rivers. The immature stages always occur in riffle habitats, usually where current velocities are 1-1.5m/s. Larvae and pupae typically coexist with blephariceriids, including one or more of the following species: *Agathon comstocki*, *Blepharicera jordani*, *B. ostensackeni* Kellogg, and *Bibiocephala grandis*.

As is typical of most species, *D. coloradensis* adults emerge early in the morning, with the emergence period usually lasting *ca.* 1 hour. Flight behaviour of *D. coloradensis* is similar to other species (*e.g.*, *D. vernalis*), with most adult activity immediately over the stream surface (see chapter 5; Arnaud 1974; Turner *et al.* 1986). Live, wingless females are sometimes collected in larval habitats, suggesting active oviposition on submerged substrates. Fecundity estimates ranged from 70-160 eggs / female pupa (106.1±21.1; N=53) and was correlated with pupal size (see chapter 5).

Most *D. coloradensis* populations are univoltine but relatively asynchronous, with larvae, pupae and adults often present for 3-4 months. The remainder of the year, including the overwintering period, is passed in the egg stage. Data for some populations suggest that several generations may be produced at some sites (see chapter 5).

Remarks: Most Nearctic species exhibit consistent morphological characters that allow differentiation of at least larvae and pupae. However, many of these taxonomically compelling characters demonstrate marked polymorphism in *D. coloradensis*. Larval cranial color is much more variable than in other species, ranging from a mostly pale to predominantly dark pattern (*cf.* Figs. 6-8). Pupal mesothoracic spines, which are consistent, diagnostic features of other species (*e.g.*, *D. shasta*, *D. personata*), occur in some populations of *D. coloradensis* (Fig. 19; see below), and mesothoracic tubercles, primary characters used in Kennedy's (1958, 1960) pupal keys, may be absent, moderately developed, or pronounced and with darkly sclerotized apices. Adult characters, particularly male genitalia (*e.g.*, shape of dorsal plate), may also be quite variable (*cf.* Figs. 79, 80). In certain populations, and sometimes across broad geographic zones (*e.g.*, Cascade Range of Oregon and Washington), larval, pupal and adult characters can be relatively constant. Several geographically distinct morphotypes can be recognized from western North America, suggesting the presence of more than one species. However, because of the distribution and prevalence of intermediate or highly variable populations, all morphotypes are considered conspecific.

Since first discovered in May, 1942, mountain midges from Benton Co., Oregon have remained an enigma. The original sample contained a single larva from Rock Creek, a tributary of the Marys River, southwest of Philomath. Pennak (1945) found the specimen indistinguishable from larval *D. coloradensis*, but acknowledged that "a more reliable identification" required pupal examination. The first pupa, collected in April, 1947 "north of Peoria slough"[1], was identified by Stone (1949) as *D. coloradensis*. However, because the specimen possessed distinct mesothoracic spines (*cf.* Fig. 19), Wirth (1951) believed the specimen was conspecific with *D. shasta*. Additional larvae and pupae were collected by V.D. Roth, Oregon State College, in tributaries of the Alsea and Marys Rivers (Kennedy, 1958). Most pupae possessed mesothoracic spines, but both Kennedy (1960) and Roth (1981, *personal communication*) believed the spines were distinctly different from those of *D. shasta*, and that the specimens represented a new species.

As more specimens and ecological information have become available, the status of the spined pupal morphotype has become even more difficult to interpret taxonomically. At present, this morphotype has been found in only four watersheds, all in the Coast Range of Oregon. It is widespread and abundant in the Marys River (Benton Co.) and Clatskanie

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[1] The specimen was apparently collected in the Willamette River, ca. 5 mi above the confluence of the Marys River.

River (Columbia Co.) watersheds, and relatively rare in the Alsea River (Benton Co.) and Salmonberry River (Tillamook Co.) watersheds. Unspined pupae, indistinguishable from *D. coloradensis*, also occur at the first 3 sites, with this morphotype prevalent in the Alsea watershed (*e.g.*, only 5 of 467 specimens collected in 1986 had mesothoracic spines). Although unspined pupae have not been collected from Salmonberry River, the small sample size (N=5) prevents any convincing predictions about the presence of this morphotype. Intermediate specimens, with rudimentary spines, posteriorly curved spines, or spines on only one side of the mesothorax, are occasionally found in the Marys and Clatskanie watersheds, suggesting spined- and unspined morphotypes are not reproductively isolated. Of the almost 1000 specimens (pupae and larvae with well-developed pupal histoblasts) examined from the Marys watershed, *ca.* 60% possess spines, 25% lack spines, and 15% show intermediate conditions. There is no apparent correlation between spine presence and the gender, size, or temporal characteristics of the specimen. [illegible]skanie River data are based on approximately half as many specimens, all collected in May, 1986. These data indicate that *ca.* 50% of the specimens possess some type of spine (including intermediates) and, in contrast to Marys River data, there appears to be a relationship between spine presence and the gender of the specimen. Although the overall sex ratio was *ca.* 1:1, the ratio for both spined males : spined females and unspined females : unspined males was *ca.* 2:1. It is perhaps significant that all spined pupae collected from the Alsea watershed were males.

Through dissections and rearings, numerous spined-, unspined-, and intermediate pupae have been associated with larvae and adults; however, examination of larval and adult characters has not resolved the problem. Due to lack of distinguishing features in these life stages, the presence of pupal intermediates, and evidence that spine expression may be related to sex (in some populations), the spined pupal morphotype is considered conspecific with *D. coloradensis*.

As discussed above, structure of the pupal gill has shown that material identified by Kennedy (1960) as *D. nielsoni* includes specimens of *D. coloradensis*. Among these was material from Laurel Creek, California. All pupae from this locality, including those from Kennedy's synoptic collection, demonstrate a *coloradensis*, rather than *nielsoni*, type of gill, indicating that Laurel Creek mountain midges are *D. coloradensis*.

Certain streams in the Coast Range of Oregon contain larvae and pupae with prominent dorsal abdominal tubercles (Figs. 8, 20). The distribution of these morphotypes may be related to substrate, because abdominal tubercles are expressed only at sites with sedimentary substrates, and there is a positive correlation between tubercle size and the prevalence of sedimentary substrate (see chapter 5). In other respects, these populations are indistinguishable from those of *D. coloradensis*; therefore, the tubercled morphotype is considered conspecific with *D. coloradensis*.

4.5.3.15 Unplaced species of *Deuterophlebia*

4.5.3.15.1 *Deuterophlebia* sp. A

Deuterophlebia mirabilis Brodsky, 1930: 289.

Remarks: As noted above (*re. D. mirabilis*), material described as *D. mirabilis* by Brodsky (1930) is here referred to as *Deuterophlebia*. sp., partly because immature stages have not been definitively associated with the *D. mirabilis* type series, or with *D. mirabilis* males from near the type locality.

4.5.3.15.2 *Deuterophlebia* sp. B

(Fig. 10)

Deuterophlebia sp. Singh, 1961: 109.

Deuterophlebiidae Dubey and Kaul, 1971: 47.

Description

Larva (Fig. 10): Dorsal color: body dark brown. Dorsal cranium (instar IV), including clypeus and mandible base, dark brown. Distal antennal article relatively dark, but without digitiform microtrichia; pit-like sensillum near apex of ventral branch. Chaetotaxy: *prl* (as in Fig. 3), *pm* (Fig. 10), *at* and *mt* (as in Fig. 4a) simple setiform sensilla; *sbt* (meso- and metathorax) lanciform sensilla (Fig. 10); *ap* with two clusters of digitiform sensilla (as in Fig. 4a), without setiform sensilla. Measurements:

Instar	Sample size	Total length (mm)	Cranial width (mm)	Crochet rows	Antennal ratio
III	3	2.8-3.2 (3.05±0.23)	0.48	6-9	1:13:3
IV	5	2.8-4.8 (3.74±0.73)	0.70-0.74 (0.72±0.02)	10-14	1:5:1

Pupa: Unknown.

Adult : Unknown.

Material examined: INDIA, NW Himalaya: S slope of Hampta Pass, headwaters of Alhni R, Sta. 11, 4000m [ca. 32°15'N 77°15'E], 30.V.70 (*Kaul & Dubey*) [6L]; Chandra Valley, 12,000' [ca. 32°15'N 77°15'E], 8.VI.1955 & 10.VI.1955 (*M.S. Mani*) [2L].

Distribution: Known from the Pir Panjal Range and Great Himalaya (Singh 1961).

Bionomics: Singh (1961) and Dubey and Kaul (1971) provide a brief discussion of the larval habitat in the northwest Himalaya. Larvae apparently were collected in meltwater torrents, in association with Simuliidae, Blephariceridae, and other torrenticolous insects.

4.5.3.15.3 *Deuterophlebia* sp. C

(Fig. 25)

Description

Larva: Unknown.

Pupa (Fig. 25): Male antennal sheath coiled around periphery of ventral abdomen twice, terminated near head. Gill base thick, short, *ca.* twice as long as wide; gill with thick, short, posteriorly projected lobe or filament, and three elongate filaments, with two of the latter three (posterior-most pair) typically borne on a common base. Mesothoracic tubercle on dorsal, anterolateral margin of mesonotum, dorsad and slightly posterior to gill base; each tubercle extended anterolaterally in form of 2 stout spines; spines broadly united basally, tapered apically to near outer margin of gill. Mesonotal bands transverse, raised, darkly sclerotized, between thoracic tubercle and ecdysial line; anterodorsal mesonotum with 2-3 small, raised, darkly sclerotized dots on either side of ecdysial line. Metanotal bands similar to mesonotal bands, but less darkly sclerotized and shorter. Abdominal segments I, II, VI and VII laterally with 12, 16-20, 5 and 11 thorn-like spines, respectively.

Microsculpture: Mesonotum rugose; meso- and metanotum irregularly set with ovoid microtubercles [apparently][1] bearing apical microtrichia. Abdominal sutures simple, without secondary ridges; tergites with microtubercles bearing dense apical microtrichia; adjacent cuticle apparently glabrous.

Measurements. Male pupa (N=1): Total length 3.24mm, width 2.40mm.

Adult : Unknown.

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[1] Light microscopical examination of both thoracic and abdominal cuticle demonstrates a microsculptural arrangement similar to *D. inyoensis*, with microtrichia appearing as a corona around the microtubercle; this suggests microtrichia are situated in an apical position, although definitive confirmation may require SEM examination.

Material examined: NEPAL, Tributary to Dudh Kosi, south of Tengboche, 29.X.1973 (*K.D. & S.F. Kimball*) [1 P]; slide-mounted in Canada Balsam [USNM].

Distribution: Known only from Nepal.

Remarks: The presence of two spines on each side of the mesothorax suggests that this species may be a close relative of, or even conspecific with, *D. tyosenesis*. However, the Nepal pupa and *D. tyosenensis* are markedly different in other respects (especially microsculpture, size, and distributions), suggesting they are separate taxa.

4.6 Discussion

The Deuterophlebiidae are characterized by a variety of unusual morphological and ecological features, most reflecting specialization to montane aquatic habitats. In spite of their aberrant structural features, mountain midges exhibit comparatively little intrafamily variation. Character systems known for their complexity and diversity in other insect families (*e.g.*, genitalia) are relatively simple and homogeneous in the Deuterophlebiidae. The structural homogeneity of included species and concomitant difficulty in identifying taxonomically useful character systems undoubtedly have contributed to the paucity of detailed investigations of the family. As with previous reviews (*e.g.*, Kennedy 1960), this research has shown that larvae and adults exhibit relatively few taxonomically useful characters, with pupae perhaps the most important life stage for differentiating species; however, this study differs from previous investigations with regard to which character systems are of greatest taxonomic utility.

Pupal macrosculpture (*e.g.*, mesothoracic spines) is a consistent and diagnostic character in some species, including *D. bicarinata*, *D. sajanica*, *D. shasta* and *D. personata*; however, these features are markedly variable in some *D. coloradensis* populations. These anomalous morphological trends are difficult to explain, partly because the function of pupal mesothoracic spines is unknown. One hypothesis is that spines are anti-predation devices. This theory seems unlikely, particularly since most predators of deuterophlebiid pupae (*e.g.*, *Rhyacophila* larvae) typically pierce the abdomen (*personal observation*). Another, perhaps more plausible, hypothesis is that mesothoracic spines modify water flow around the pupal thorax, especially near the gills. Potential benefits of flow alteration include removal of debris from, or increased oxygen delivery to, the gill surface. Observations of the pupal habitat of Nearctic species fail to support a relationship between spine presence and stream turbidity or oxygen levels. However, this pattern does not necessarily falsify the hypothesis, since the selective pressures effecting evolution of mesothoracic spines, be they predation, turbidity, oxygen, or some other parameter, may no longer be reflected in contemporary habitats. It is hoped that future investigations will examine flow near the pupal gills, to test whether or not mesothoracic spines effect sedimentation of, or oxygen delivery to, the gill surface.

Insights into the function of other macrosculptural features come from ontogenetic data. Several features of the pharate pupa, including prothoracic spines (if present), transverse meso- and metanotal bands, and lateral spines on abdominal segments I, II, VI and VII, are visible through the cuticle of a mature instar IV larva. Immediately after ecdysis, most pupal cuticle is pale and soft, and *ca.* one hour is needed for sclerotization (Kennedy 1958). However, the lateral abdominal spines, transverse thoracic bands, and prothoracic spines are darkly sclerotized at ecdysis, apparently because of pre-hardening of pupal cuticle. Pre-hardening of cuticle is typical of structures required immediately after molting, including mouthparts, leg joints, and muscle apodemes. An immediate use assumption may provide insights about the function of pre-hardened pupal structures in deuterophlebiids. Brodsky (1930, pg 305) speculated that the lateral spines on abdominal segments I, II, VI and VII help secure the transforming "Larve-Puppe" to the substrate, while adhesive discs are forming on the ventrolateral abdomen. It is possible that lateral abdominal spines may accrue some hydrodynamic or anti-predation function; however, these explanations seem less compelling than Brodsky's. The need for temporary attachment devices, while the more permanent adhesive discs are being formed, better explains the requirement for pre-hardened, immediately functional, lateral abdominal spines. Fully developed, sclerotized, transverse thoracic bands are also evident at the instar IV - pupal molt. The mesonotal bands of a pharate pupa are situated within the larval prothorax, in a zone where the larval cuticle ruptures at the onset of ecdysis; examination of specimens captured at various stages of eclosion suggests that mesonotal bands may assist the eclosion process by abrading against and piercing the larval cuticle. Additionally, both the meso- and metanotal bands may provide rigidity to the pupa during sclerotization of the general body surface. More extensive transverse cuticular banding, even on abdominal tergites, is evident in certain Palaearctic species (*e.g.*, *D. bicarinata*, *D. nipponica*).

Other pupal characters, including gill structure and abdominal microsculpture, are diagnostic for some Nearctic species. Except for filament number (Jedlicka and Halgos 1981), features of the pupal gill have not been used in previous taxonomic analyses. This study has shown that gill structure is diagnostic of some species (*e.g.*, *D. inyoensis*), and allows greater taxonomic resolution of other species (*e.g.*, *D. nielsoni*). Although microsculptural peculiarities of deuterophlebiid pupae were noted by Kitakami (1938b) and Kennedy (1958, 1960), the present analysis is the first demonstration that the character system is useful for species identification.

Larvae and pupae are unknown for many species (*i.e.*, Palaearctic taxa), with differentiation of these taxa dependent primarily on adult characters. Males of some species are recognized by genitalic features (*e.g.*, shape of dorsal plate - *cf.* Figs. 73-78); however, the same characters may be quite varied in other species (*e.g.*, *D. coloradensis* - *cf.* Figs. 79-80), leading one to question their general taxonomic utility. Compared to the structurally homogeneous adults of Nearctic species, those of Palaearctic species demonstrate rather aberrant and distinctive characters; this is especially true of *D. brachyrhina*, *D. oporina*, *D. blepharis*. If and when the immature stages of these flies are discovered, it is likely that they, too, will exhibit unusual features, especially considering they seem to be among the most primitive deuterophlebiids (see chapter 6).

Antennal and leg characters of adult males are of minor importance for separating species, mostly serving to identify *D. brachyrhina*, *D. oporina*, and *D. inyoensis*. However, these structures deserve comment under the context of morphological adaptations of adult mountain midges. Males possess several unusual features, including an elongate antennal flagellomere six, capitate macrotrichia on the ventral margin of the tibia and tarsus, and modified acropod, bearing a large, flattened empodium and single, ill-developed claw. These structures were described more than 65 years ago (Edwards 1922), but their functional significance has remained an enigma. I propose that these features are adaptations to the males' exclusively aerial existence above torrential habitats. Male deuterophlebiids generally fly at or near the stream surface, usually over turbulent reaches, and imagos are frequently knocked into the water. Recovery from these events is usually rapid, with males able to break free from the stream surface and resume flight within a few seconds (*personal observation*). This ability is probably related to the mechanical and hydrofuge properties of elongate appendages, particularly those bearing capitate macrotrichia (*i.e.*, legs). Similar structures, including long, filiform antennae, and legs with enlarged empodia or without tarsal claws, are demonstrated by males of some surface-skating chironomids (Oka 1930; Tokunaga 1932; Hashimoto 1976); as in deuterophlebiid males, these chironomids are not adapted for terrestrial walking (Hashimoto 1976). Although the distal antennal flagellomere of a male deuterophlebiid bears relatively few sensilla, the elongate appendage may play a sensory function, perhaps related to swarm formation and behaviour.

This study represents the first comprehensive taxonomic treatment of the Deuterophlebiidae in almost 30 years. It has introduced several new character systems, evaluated the taxonomic concepts of Pennak (1945, 1951), Wirth (1951), Jedlicka and Halgos (1981), and Kennedy (1958, 1960), and described new Palaearctic and Nearctic species. New data about problematic deuterophlebiids from western Oregon (Benton Co.) indicate that these populations are an aberrant morphotype of *D. coloradensis*. This widespread taxon may actually represent a complex of sibling species, elucidation of which may require laboratory cross-breeding, cytological, electrophoretic, and/or biochemical studies. This research has provided the groundwork and, hopefully, the impetus for such a supplemental investigation.

Figures 1-4. *Deuterophlebia* larvae, dorsal view.

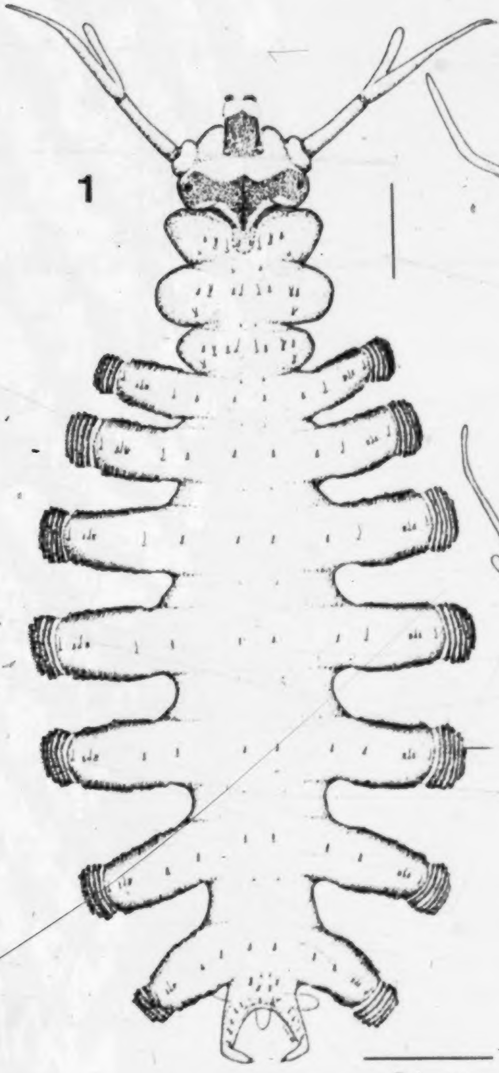
Figure 1. *Deuterophlebia personata*, habitus of instar IV larva; scale bar = 0.5mm.

Figure 2. *Deuterophlebia vernalis* instar IV larva, head, thorax, abdominal segment I; scale bar = 0.5mm.

Figure 3. *Deuterophlebia shasta* instar IV larva, head, thorax, abdominal segment I; scale bar = 0.5mm.

Figure 4. (**a**) *Deuterophlebia inyoensis* and (**b**) *D. vernalis* instar IV larvae, abdominal segments VII, VIII; scale bars = 0.25mm.

Abbreviations: *ap*, apical sensilla; *at*, anterotergal sensilla; *mt*, mediotergal sensilla; arrowheads, prelaterotergal (*prl*) sensilla.



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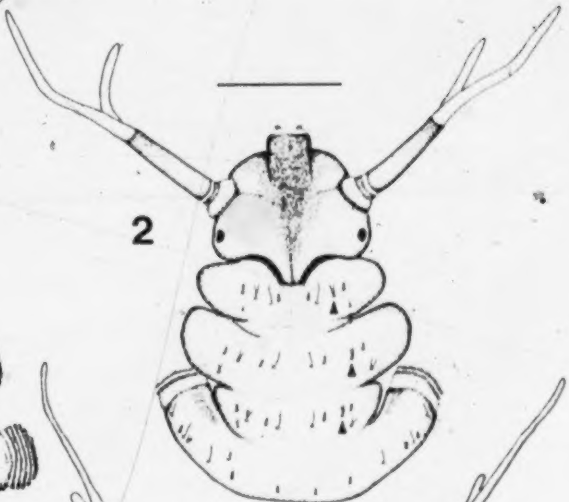

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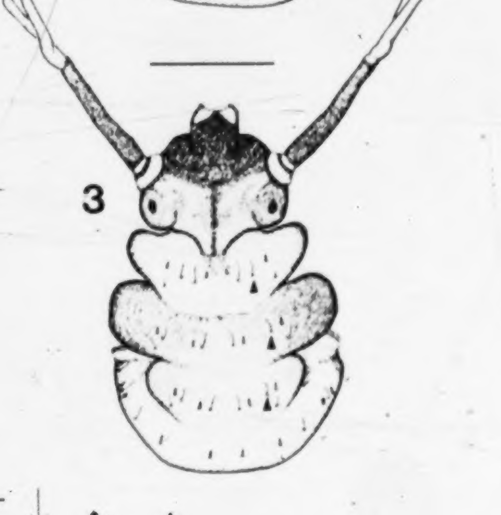

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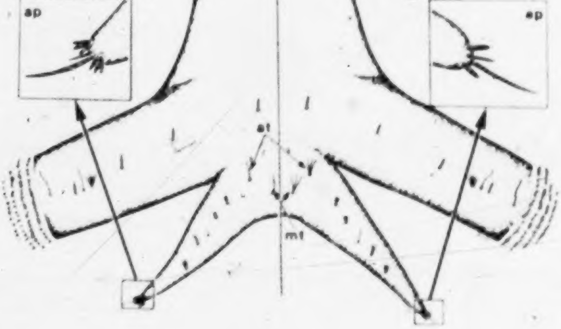


4

a
ap
at
b
ap
mt

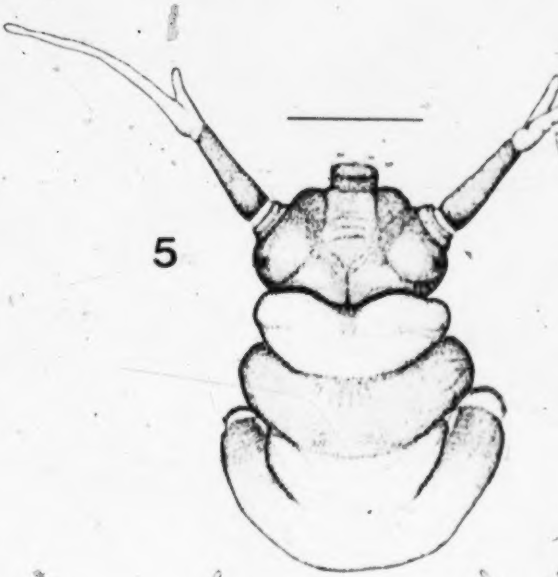
Figures 5-8. *Deuterophlebia* larvae, dorsal view; scale bar = 0.5mm.

Figure 5. *Deuterophlebia inyoensis* instar IV larva, head, thorax, abdominal segment I.

Figure 6. *Deuterophlebia nielsoni* instar IV larva, head, thorax, abdominal segment I.

Figure 7. *Deuterophlebia coloradensis* (Yukon) instar IV larva, head, thorax, abdominal segment I.

Figure 8. *Deuterophlebia coloradensis* (Oregon) instar IV larva, head, thorax, abdominal segment I; dorsal protuberances indicated by arrowheads.



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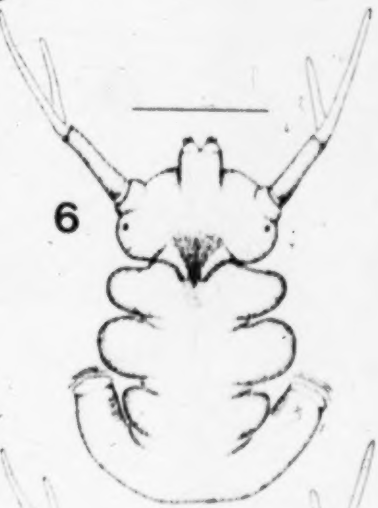

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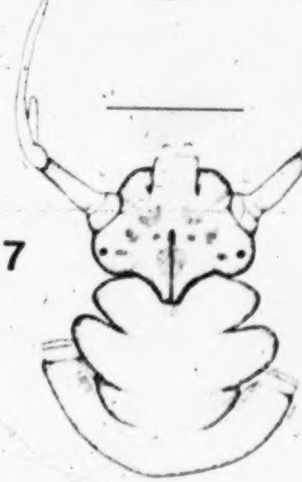

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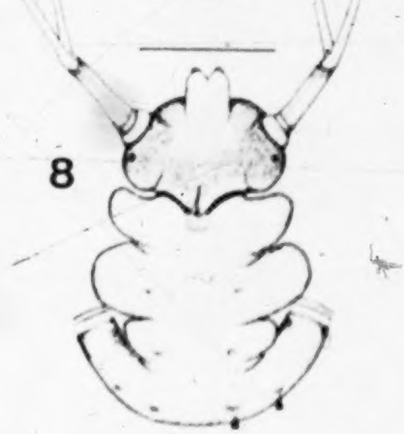

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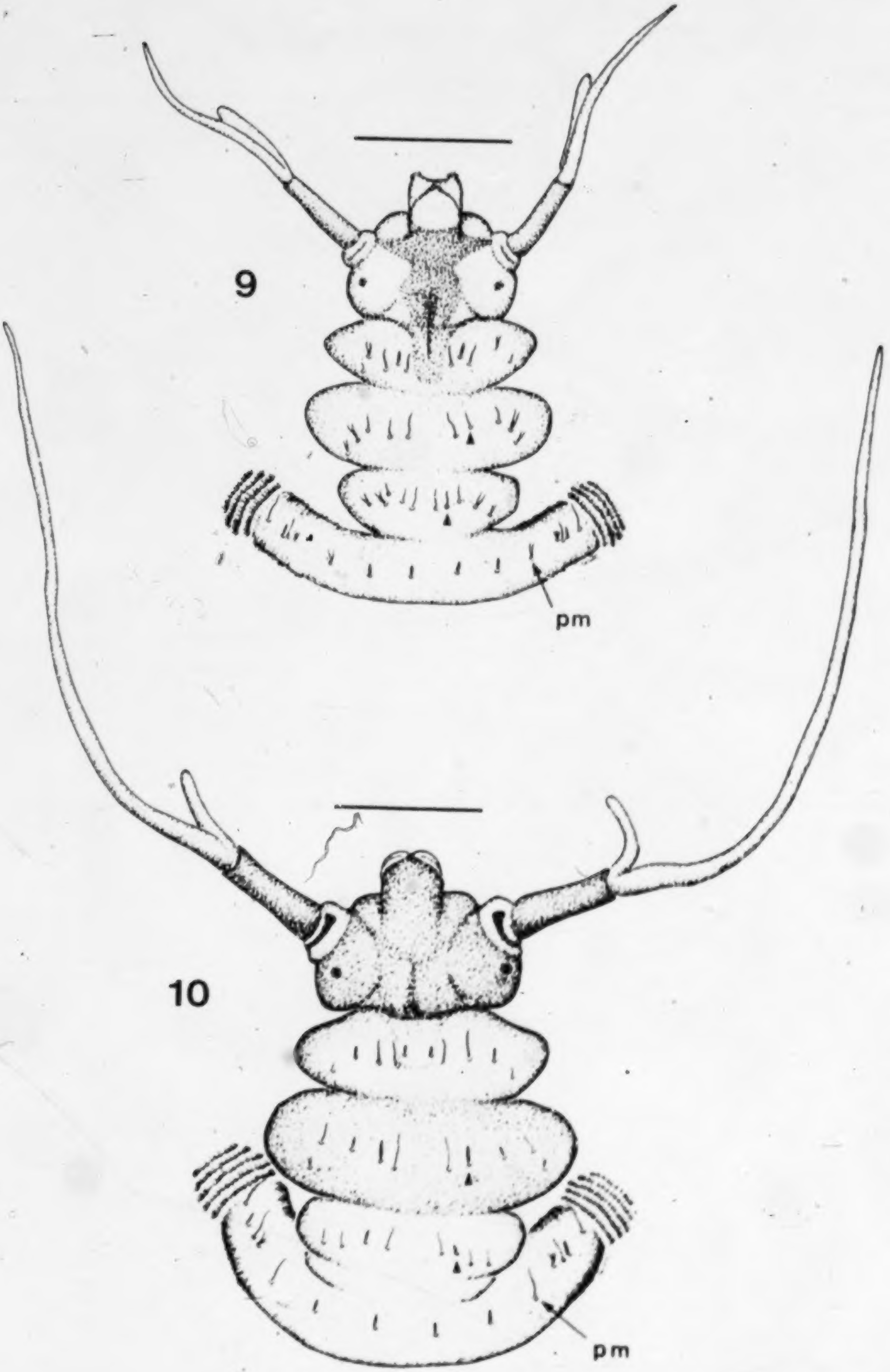
Figures 9-10. *Deuterophlebia* instar IV larvae, dorsal view; scale bars = 0.5mm.

Figure 9. *Deuterophlebia bicarinata* instar IV larva, head, thorax, and abdominal segment I.

Figure 10. *Deuterophlebia* sp. B instar IV larva, head, thorax, and abdominal segment I.

Abbreviations: *pm*, medial pseudopodal sensilla; arrowheads, subtergal (*sbt*) sensilla.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pm

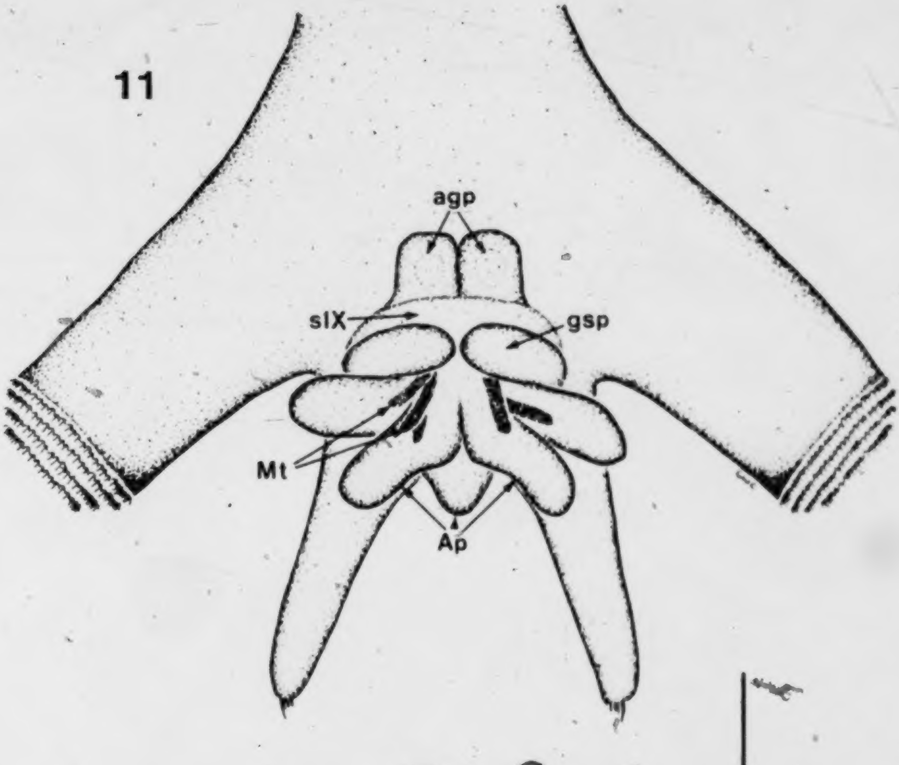
Figures 11-12. *Deuterophlebia* instar IV larvae, ventral view; scale bar = 0.2mm.

Figure 11. *Deuterophlebia personata* instar IV larva, abdominal segments VII-VIII of male, showing genitalic primordia.

Figure 12. *Deuterophlebia personata* instar IV larva, abdominal segments VII-VIII of female, showing genitalic primordia.

Abbreviations: *agp*, accessory gland primordia; *Ap*, anal papillae; *gsp*, gonostylus primordia; *Mt*, terminus of Malpighian tubules; *sIX*, pupal sternite IX primordia.

11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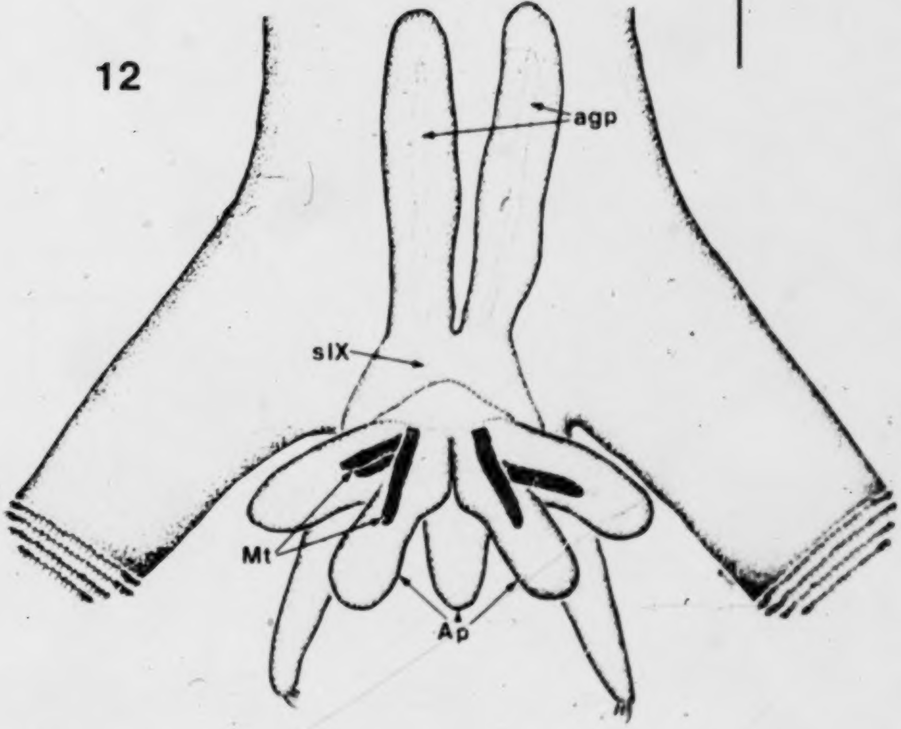
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Figures 13-14. *Deuterophlebia* pupae, dorsal (left) and ventral (right) views; scale bar = 0.5mm.

Figure 13. *Deuterophlebia personata* male pupa (ventral view with left antennal sheath removed).

Figure 14. *Deuterophlebia personata* female pupa.

Abbreviations: *ad*, adhesive discs; *an*, antennal sheath; *mes*, mesonotum; *met*, metanotum; *pro*, prothorax; *ws*, wing sheath.

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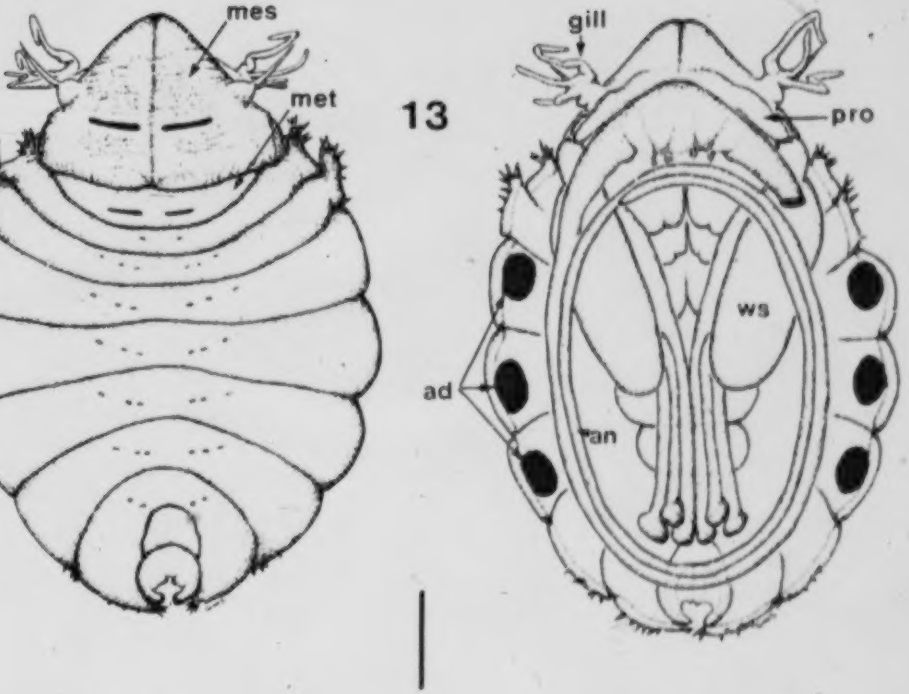
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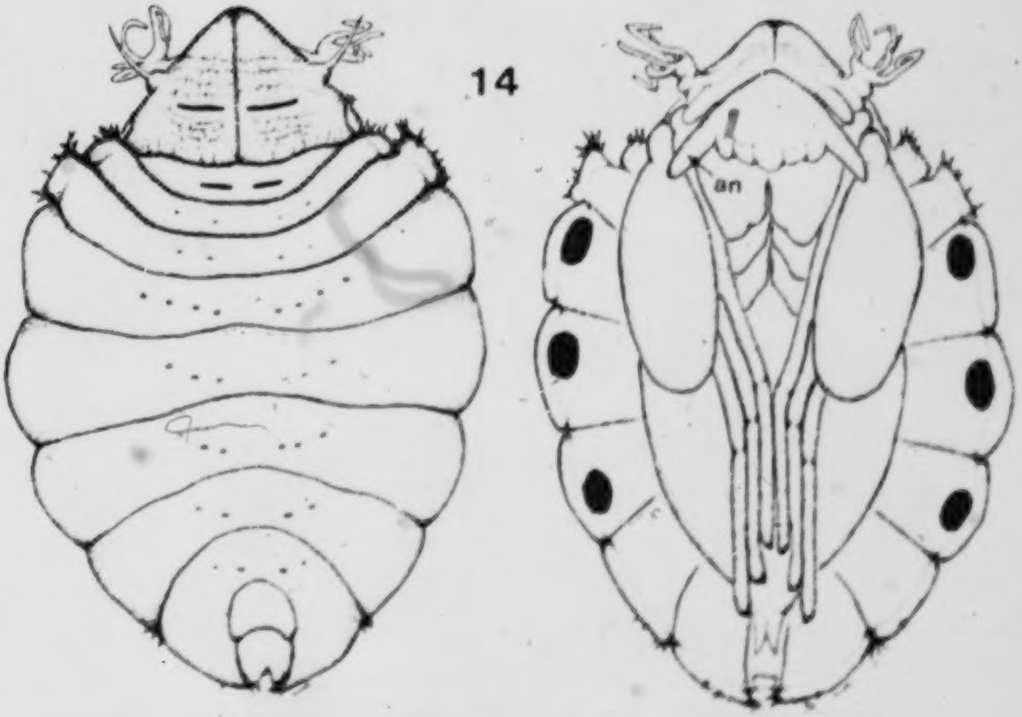


Figures 15-21. *Deuterophlebia* pupae, dorsal view of thorax, abdominal segments I, II (Fig. 20 shows entire pupa); scale bars = 0.5mm.

Figure 15. *Deuterophlebia inyoensis*, male pupa; ventrolateral protuberance indicated by arrowhead.

Figure 16. *Deuterophlebia shasta*, male pupa.

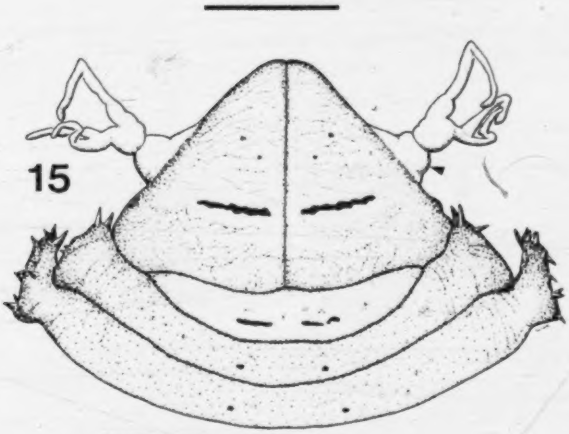
Figure 17. *Deuterophlebia nielsoni*, male pupa.

Figure 18. *Deuterophlebia vernalis*, male pupa.

Figure 19. *Deuterophlebia coloradensis* (Oregon), male pupa.

Figure 20. *Deuterophlebia coloradensis* (Oregon), male pupa.

Figure 21. *Deuterophlebia coloradensis* (Oregon), male pupa.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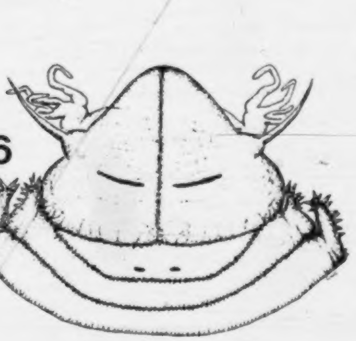
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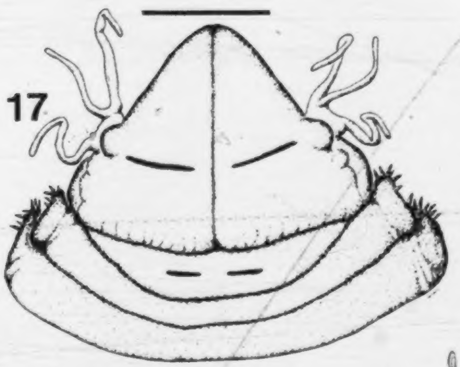
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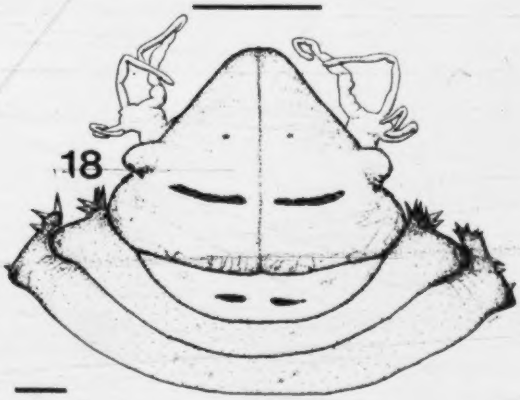
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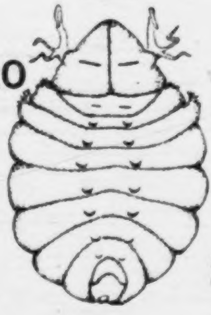
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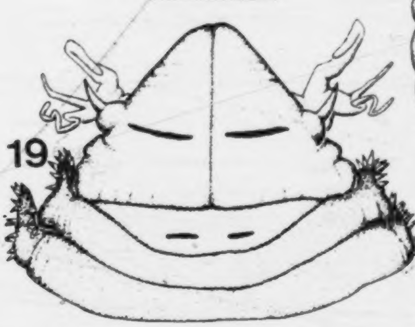
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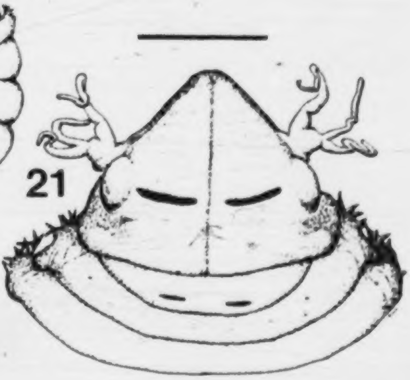
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Figures 22-26. *Deuterophlebia* pupae, dorsal view; scale bars = 0.5mm.

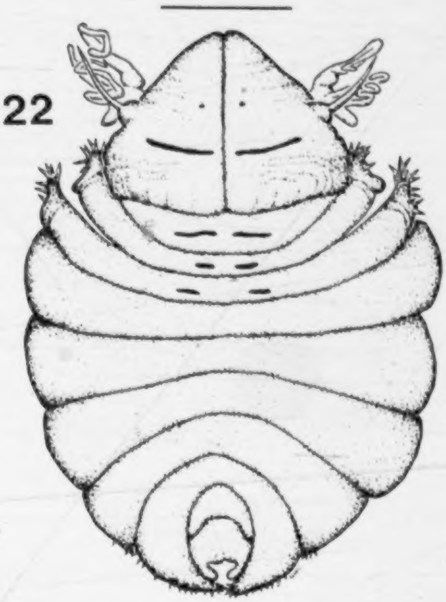
Figure 22. *Deuterophlebia bicarinata*, male pupa.

Figure 23. *Deuterophlebia sajanica*, thorax, abdominal segments I, II of male pupa.

Figure 24. *Deuterophlebia tyosenensis*, thorax, abdominal segments I, II of female pupa.

Figure 25. *Deuterophlebia* sp. C, thorax, abdominal segments I, II of male pupa.

Figure 26. *Deuterophlebia nipponica*, female pupa.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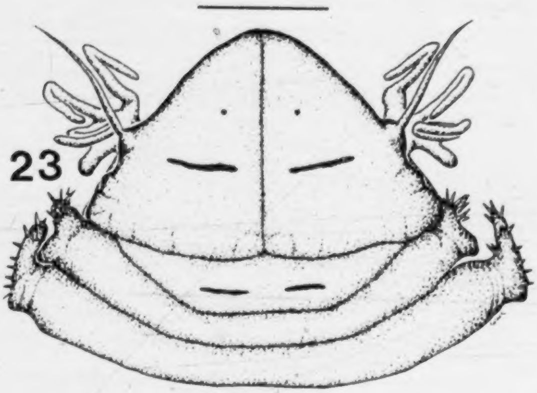
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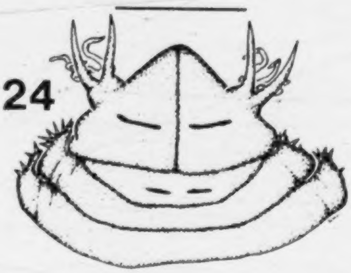
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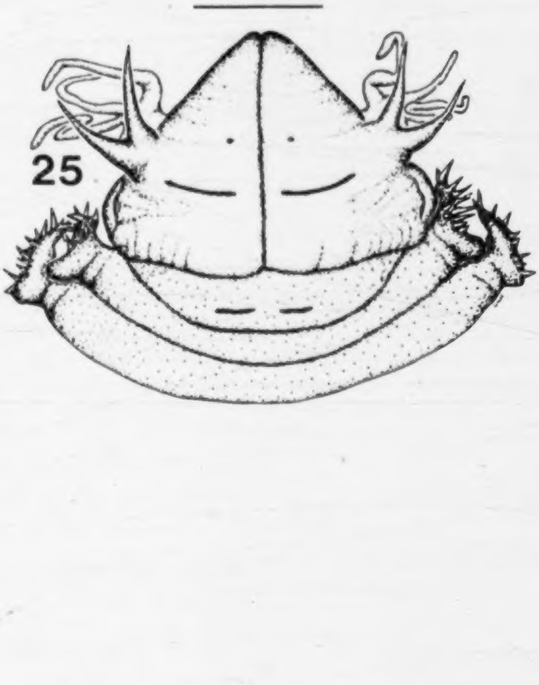
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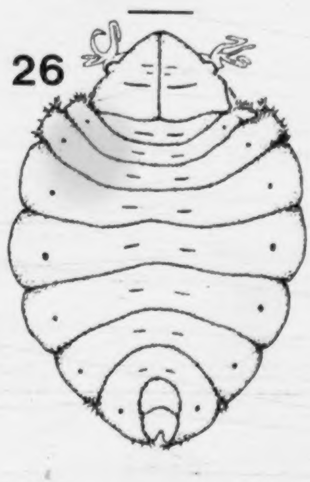
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Figures 27-30. *Deuterophlebia* pupal gills.

Figure 27. *Deuterophlebia sajanica* pupal gill.

Figure 28. *Deuterophlebia inyoensis* pupal gill.

Figure 29. *Deuterophlebia nielsoni* pupal gill.

Figure 30. *Deuterophlebia coloradensis* pupal gill.

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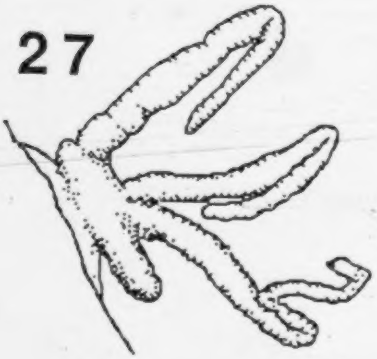

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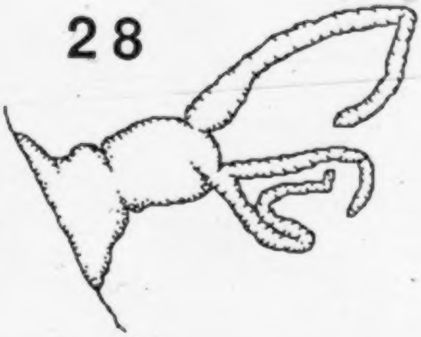

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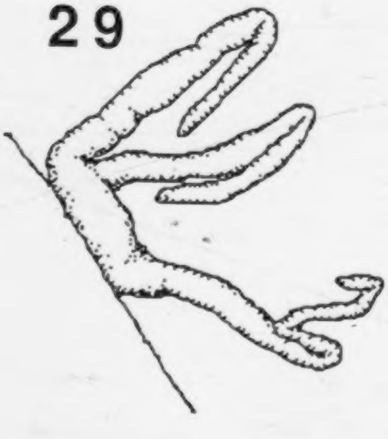

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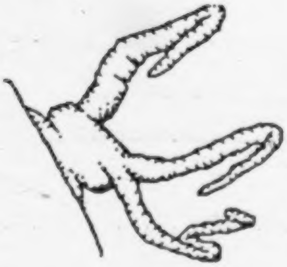


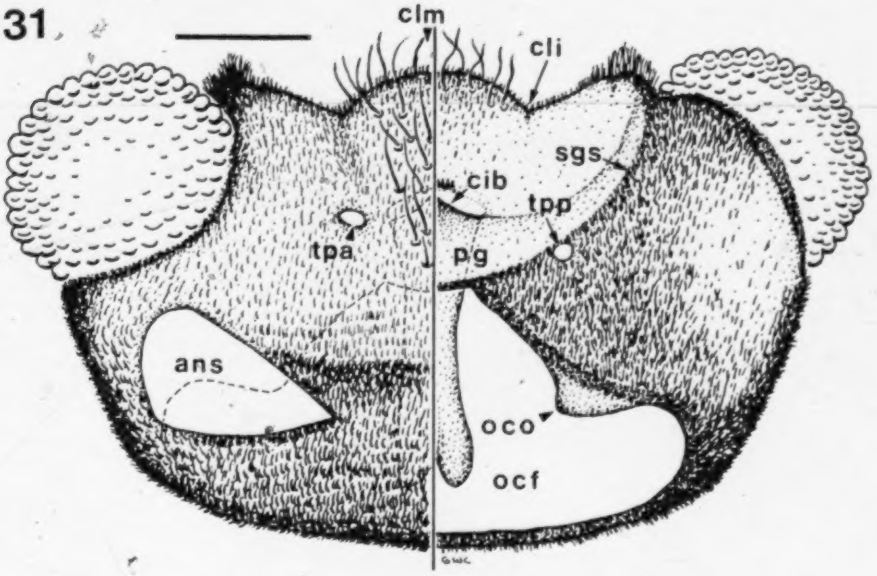
Figures 31-32. *Deuterophlebia* adult cranium, dorsal (left) and ventral (right) views (antennae removed); scale bars = 0.1mm.

Figure 31. *Deuterophlebia vernalis*, cranium of adult male.

Figure 32. *Deuterophlebia vernalis*, cranium of adult female.

Abbreviations: *ans*, antennal socket; *cib*, cibarium; *clm*, median clypeal lobe; *cli*, clypeal incision; *ocf*, occipital foramen; *oco*, occipital condyle; *pg*, postgena; *sgs*, subgenal suture; *tpa*, anterior tentorial pit; *tpp*, posterior tentorial pit.

31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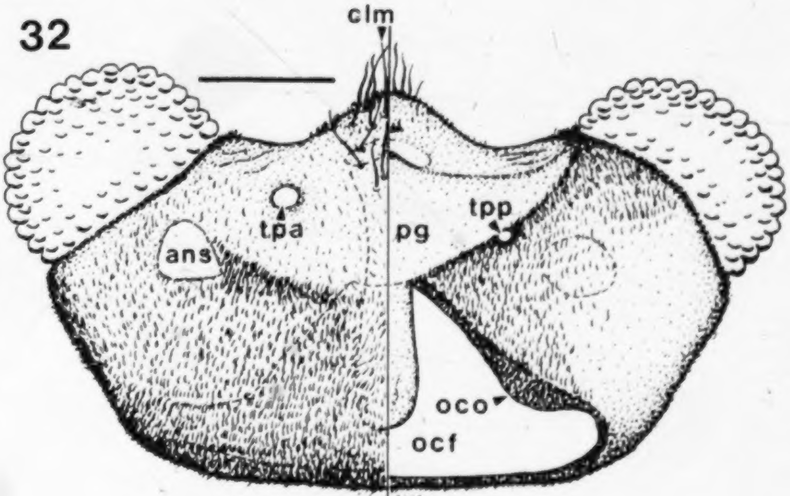
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Figures 33-34. *Deuterophlebia* adult antennae, dorsal views; scale bars = 0.1mm.

Figure 33. *Deuterophlebia vernalis*, antenna of adult male (base only).

Figure 34. *Deuterophlebia vernalis*, antenna of adult female.

Abbreviations: *f1* (to) *f4*, flagellomere 1 (to) flagellomere 4; *ped*, pedicel; *sc*, scape.

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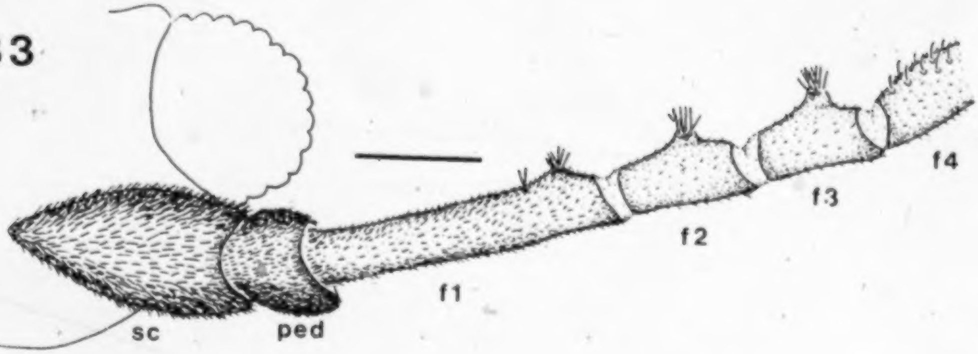
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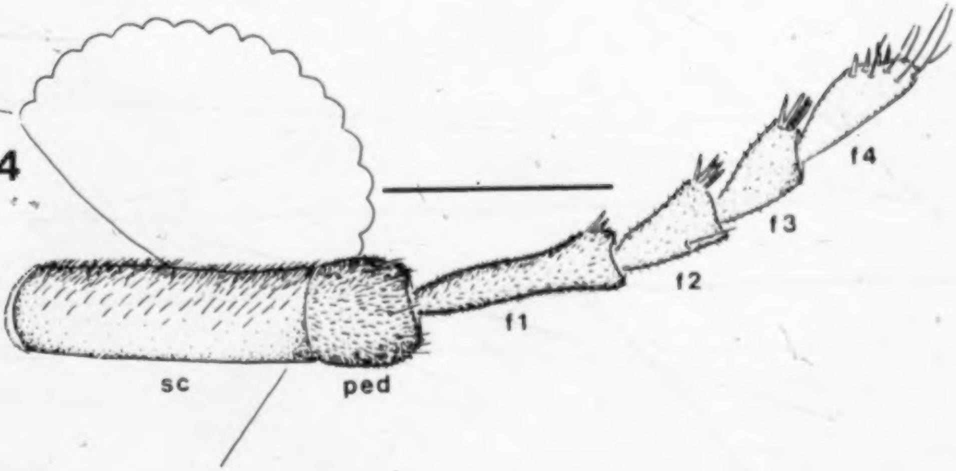
f4
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Figures 35-37. *Deuterophlebia* female genitalia, internal; scale bar = 0.1mm.

Figure 35. *Deuterophlebia vernalis*, lateral view (semi-diagrammatic) of female genitalia.

Figure 36. *Deuterophlebia vernalis*, dorsal view of genital fork.

Figure 37. *Deuterophlebia inyoensis*, dorsal view of genital fork.

Abbreviations: *ag*, accessory gland (base); *tVIII* (to) *tX*, tergite VIII (to) tergite X; *sVIII*, sternite VIII; *gf*, genital fork arms; *gfb*, anterior bridge of genital fork; *gfp*, posterior lobes genital fork; asterisk, basal opening of accessory gland.

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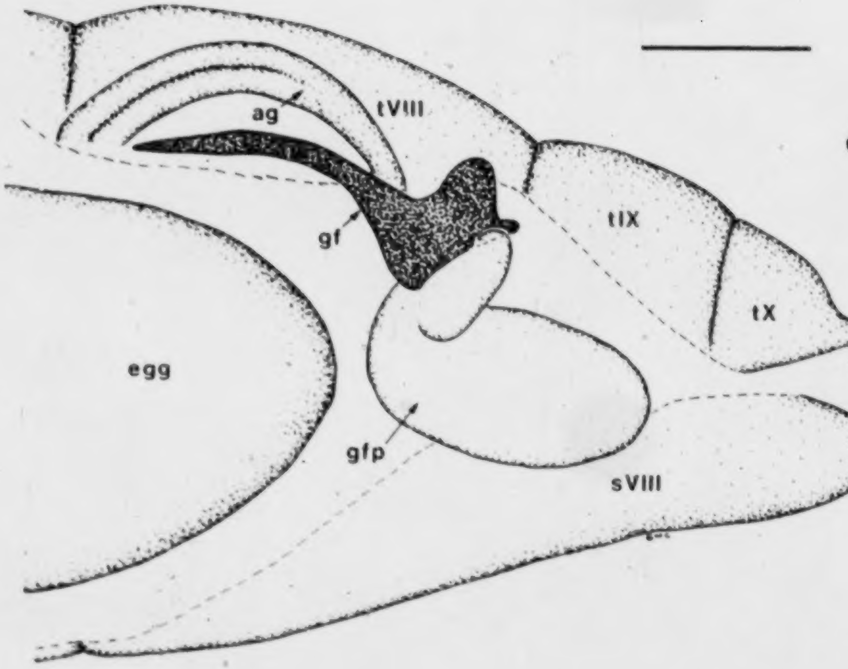
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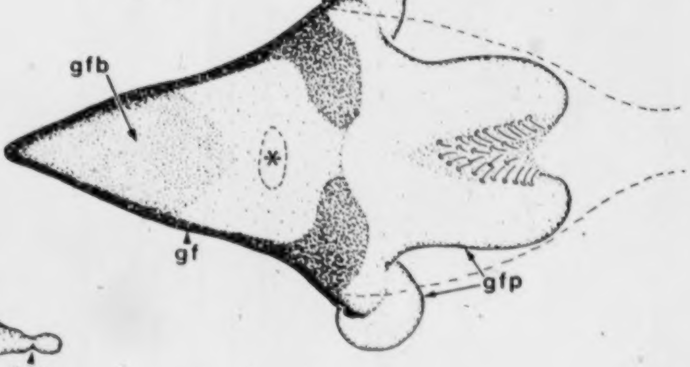

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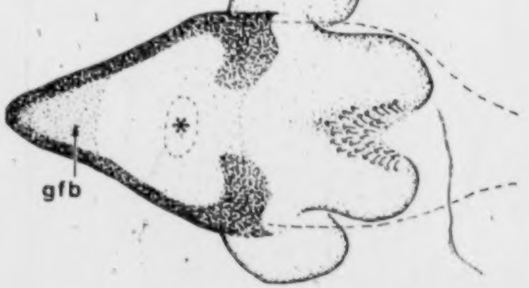

Figures 38-46. Selected characters of *Deuterophlebia* larvae and pupae.

Figure 38. *Deuterophlebia coloradensis* instar IV larva, ventral branch of distal antennal article; scale bar = 10µm.

Figure 39. *Deuterophlebia inyoensis* instar IV larva, ventral branch of distal antennal article; scale bar = 10µm.

Figure 40. *Deuterophlebia shasta*, pupal microsculpture, abdominal tergite IV (upper left) and V (lower right); secondary ridges on sutures indicated by arrowheads; scale bar = 10µm.

Figure 41. *Deuterophlebia inyoensis* pupal microsculpture, abdominal tergite VII; scale bar = 5µm.

Figure 42. *Deuterophlebia coloradensis* (Oregon) pupal microsculpture and suture, abdominal tergite IV (upper left) and V (lower right); scale bar = 10µm.

Figure 43. *Deuterophlebia personata* pupal microsculpture, abdominal tergite VI; scale bar = 5µm.

Figure 44. *Deuterophlebia nielsoni* pupal microsculpture, abdominal tergite V; scale bar = 5µm.

Figure 45. *Deuterophlebia vernalis* pupal microsculpture, abdominal tergite V; scale bar = 5µm.

Figure 46. *Deuterophlebia bicarinata* pupal microsculpture, abdominal tergite I; scale bar = 5µm.

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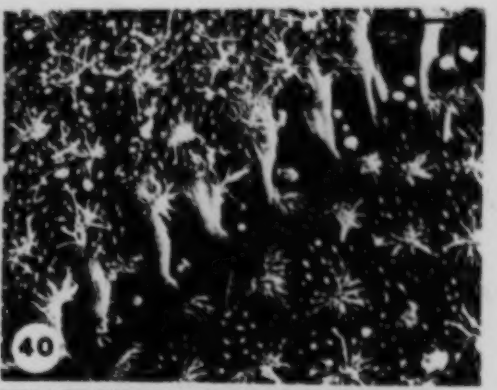
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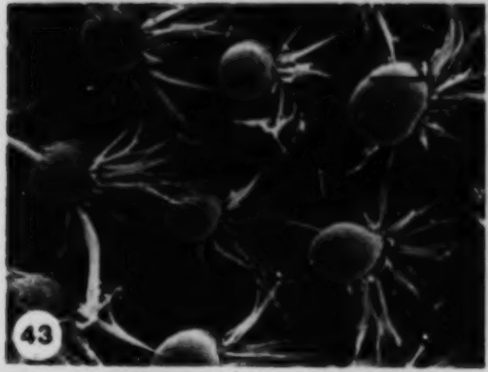
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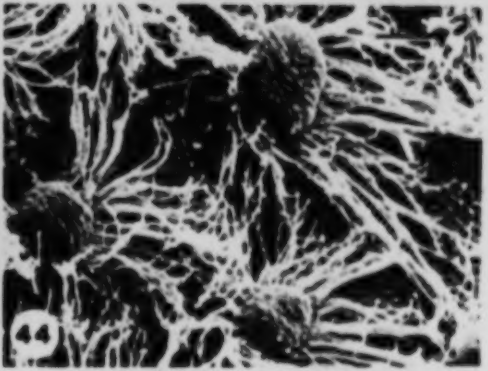
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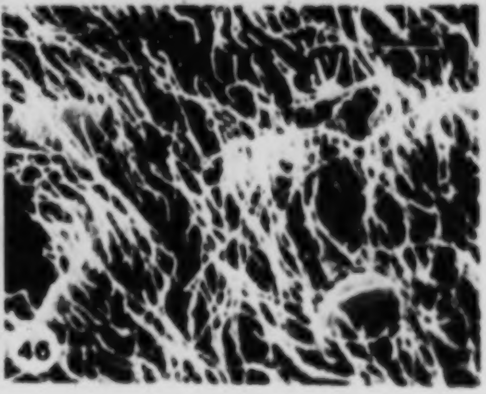

46

Figures 47-54. Selected characters of *Deuterophlebia* pupae and adults.

Figure 47. *Deuterophlebia coloradensis* pupa, abdominal tergite IX; scale bar = 50µm.

Figure 48. *Deuterophlebia vernalis* pupa, abdominal tergite IX, showing anal projection (asterisk); scale bar = 50µm.

Figure 49. *Deuterophlebia brachyrhina*, cranium of adult male (dorsal view); scale bar = 0.1mm.

Figure 50. *Deuterophlebia oporina*, cranium of adult male (dorsal view); scale bar = 0.1mm.

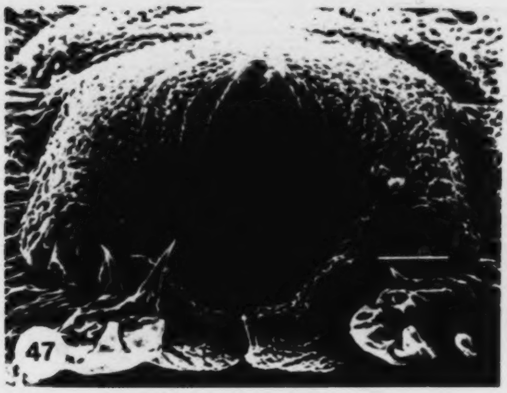
Figure 51. *Deuterophlebia shasta*, cranium of adult male (dorsal view); scale bar = 0.1mm.

Figure 52. *Deuterophlebia personata*, cranium of adult male (dorsal view); scale bar = 0.1mm.

Figure 53. *Deuterophlebia coloradensis*, cranium of adult male (dorsal view); scale bar = 0.1mm.

Figure 54. *Deuterophlebia blepharis*, compound eye of adult male (SEM of uncoated specimen); scale bar = 25µm.

Abbreviations: *clm*, median clypeal lobe; *cli*, clypeal incision; *tpa*, anterior tentorial pit.



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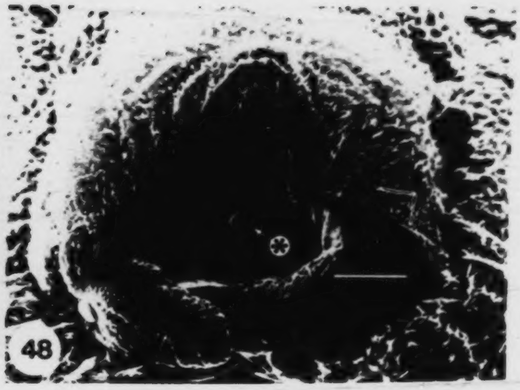

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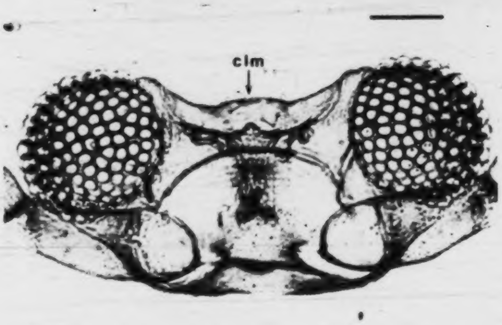

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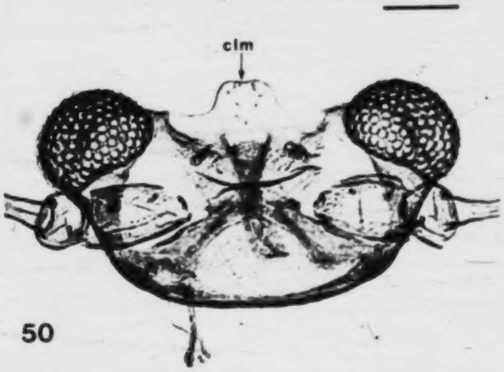

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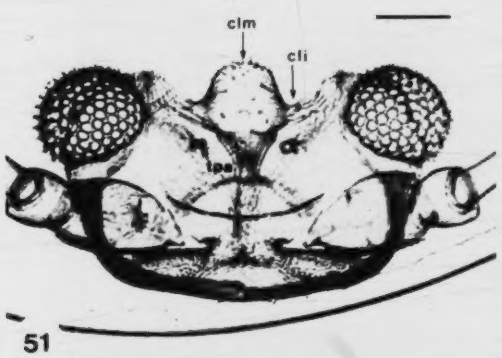

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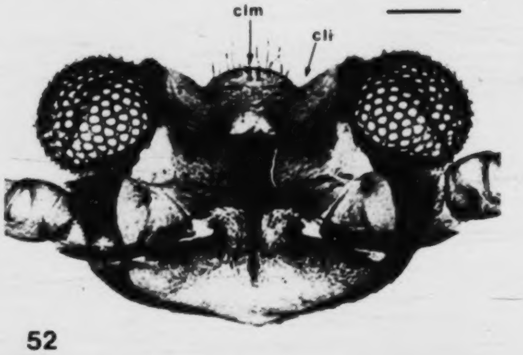

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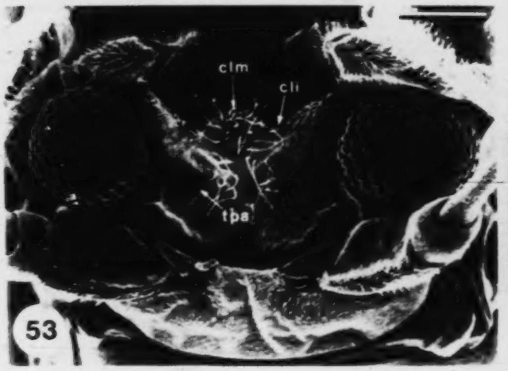

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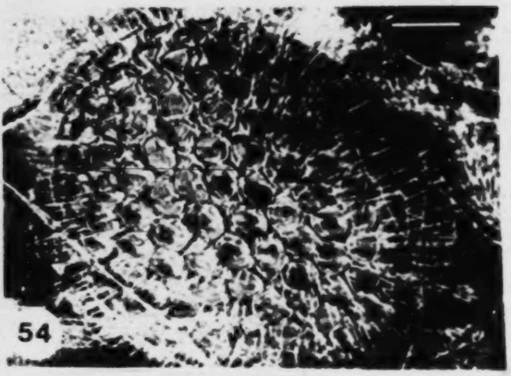

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Figures 55-64. Selected characters of *Deuterophlebia* adults.

Figure 55. *Deuterophlebia oporina*, oral region of adult male (ventral view); scale bar = 25µm.

Figure 56. *Deuterophlebia inyoensis*, oral region of adult male (ventral view); scale bar = 25µm.

Figure 57. *Deuterophlebia vernalis*, oral region of adult male (ventral view); scale bar = 25µm.

Figure 58. *Deuterophlebia personata*, distal end of foretibia of adult male; scale bar = 20µm.

Figure 59. *Deuterophlebia brachyrhina*, antennal flagellomeres 1-3 of adult male (anterodorsal view); scale bar = 40µm.

Figure 60. *Deuterophlebia inyoensis*, antennal flagellomeres 1-3 of adult male (dorsal view); scale bar = 40µm.

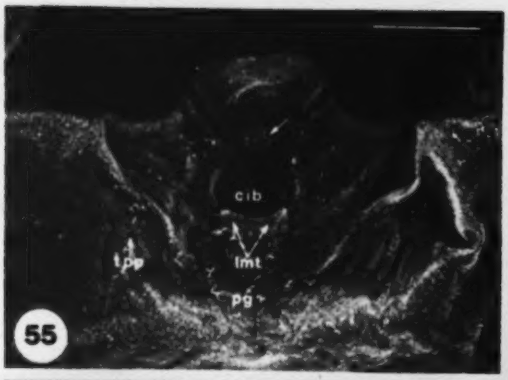
Figure 61. *Deuterophlebia coloradensis*, antennal flagellomeres 1-3 of adult male (dorsal view); scale bar = 40µm.

Figure 62. *Deuterophlebia brachyrhina*, hindtarsus of adult male (posterior view); scale bar = 50µm.

Figure 63. *Deuterophlebia brachyrhina*, distal end of foretibia of adult male; scale bar = 20µm.

Figure 64. *Deuterophlebia inyoensis*, distal end of foretibia of adult male; scale bar = 20µm.

Abbreviations: *cib*, cibarium; *f1* (to) *f3*, flagellomere 1 (to) flagellomere 3; *lmp*, labial palp; *lmt*, mental tooth; pg, postgena; *sgs*, subgenal suture; *tpp*, posterior tentorial pit; asterisk, maxillary palpi?.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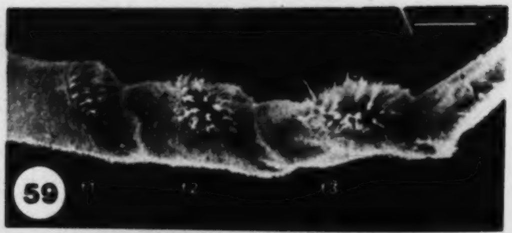
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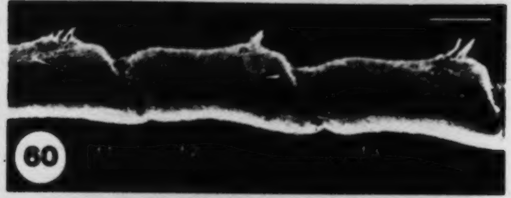
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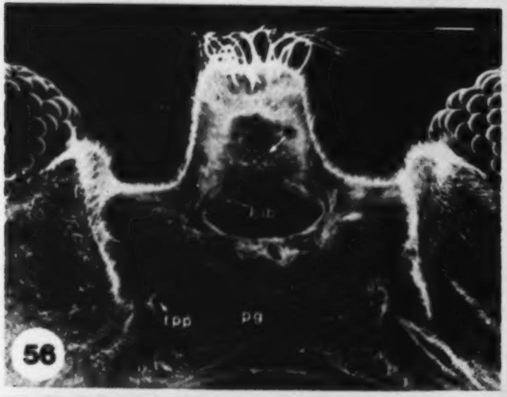
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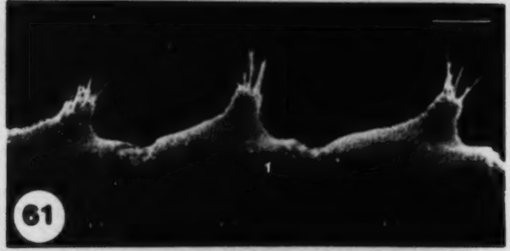
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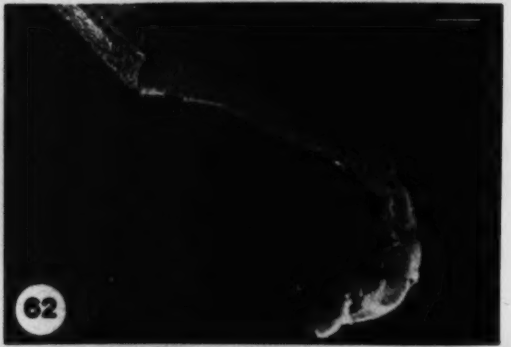
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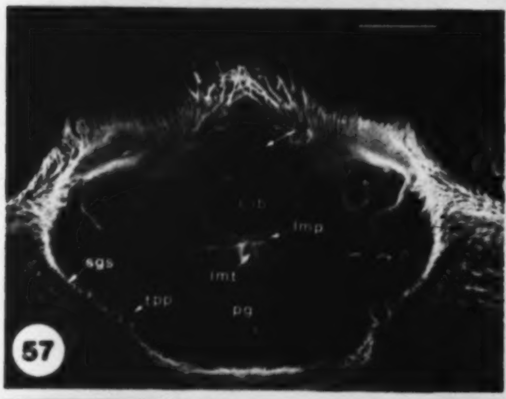
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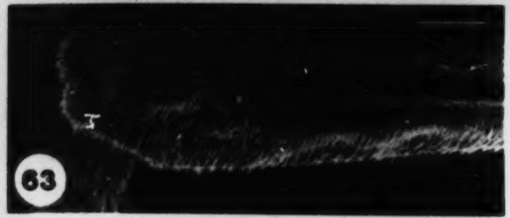
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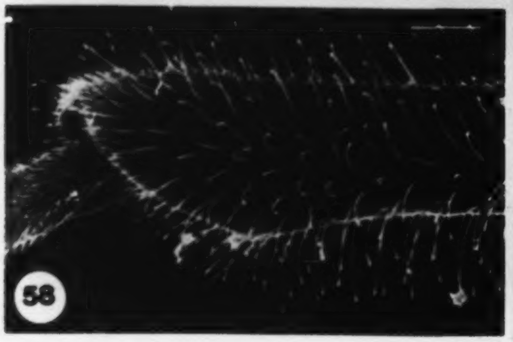
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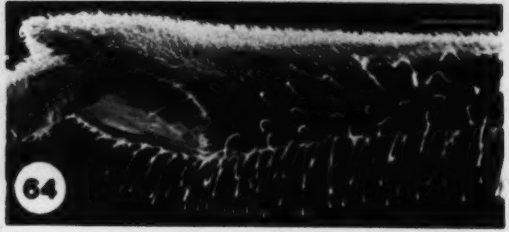
64

Figures 65-72. Selected characters of *Deuterophlebia* adults.

Figure 65. *Deuterophlebia coloradensis*, lateral view of male acropod; scale bar = 10µm.

Figure 66. *Deuterophlebia coloradensis*, ventrolateral view of female acropod; scale bar = 10µm.

Figure 67. *Deuterophlebia shasta*, dorsal view of male genitalia; scale bar = 50µm.

Figure 68. *Deuterophlebia shasta*, oblique dorsal view of aedeagus; scale bar = 50µm.

Figure 69. *Deuterophlebia inyoensis*, dorsal view of aedeagus; scale bar = 50µm.

Figure 70. *Deuterophlebia shasta*, lateral view of female genitalia; scale bar = 20µm.

Figure 71. *Deuterophlebia coloradensis* (Oregon), lateral view of female genitalia; scale bar = 20µm.

Figure 72. *Deuterophlebia personata*, lateral view of female genitalia; scale bar = 20µm.

Abbreviations: *aed*, aedeagus; *aes*, aedeagal sheath; *cer*, cercus; *dp*, dorsal plate; *emp*, empodium; *gc*, gonocoxite; *gs*, gonostylus; *sVIII*, sternite VIII; *tIX*, tergite IX; *tX*, tergite X.

65

66

dp
67

68

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Figures 73-80. Dorsal plates of adult male *Deuterophlebia.*

Figure 73. *Deuterophlebia brachyrhina*, dorsal plate of male; scale bar = 20µm.

Figure 74. *Deuterophlebia oporina*, dorsal plate of male; scale bar = 10µm.

Figure 75. *Deuterophlebia inyoensis*, dorsal plate of male; scale bar = 20µm.

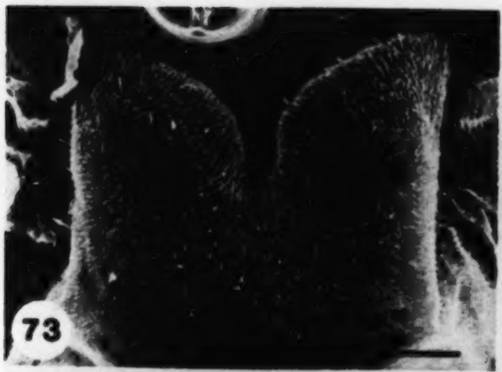
Figure 76. *Deuterophlebia mirabilis*, dorsal plate of male; scale bar = 20µm.

Figure 77. *Deuterophlebia vernalis*, dorsal plate of male; scale bar = 20µm.

Figure 78. *Deuterophlebia personata*, dorsal plate of male; scale bar = 20µm.

Figure 79. *Deuterophlebia coloradensis* (Yukon), dorsal plate of male; scale bar = 20µm.

Figure 80. *Deuterophlebia coloradensis* (Oregon), dorsal plate of male; scale bar = 20µm.



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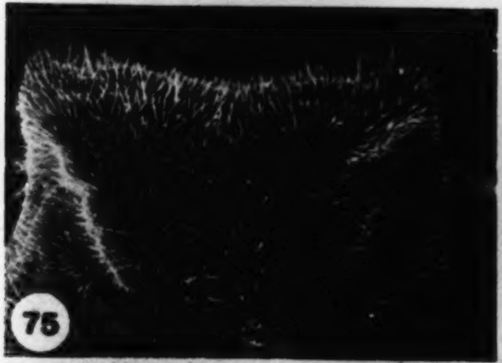

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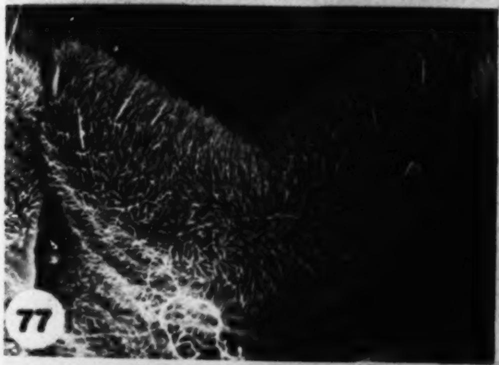

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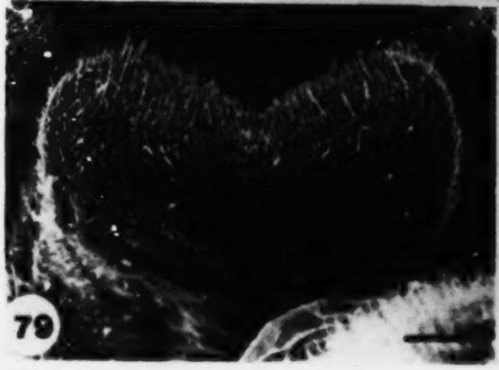

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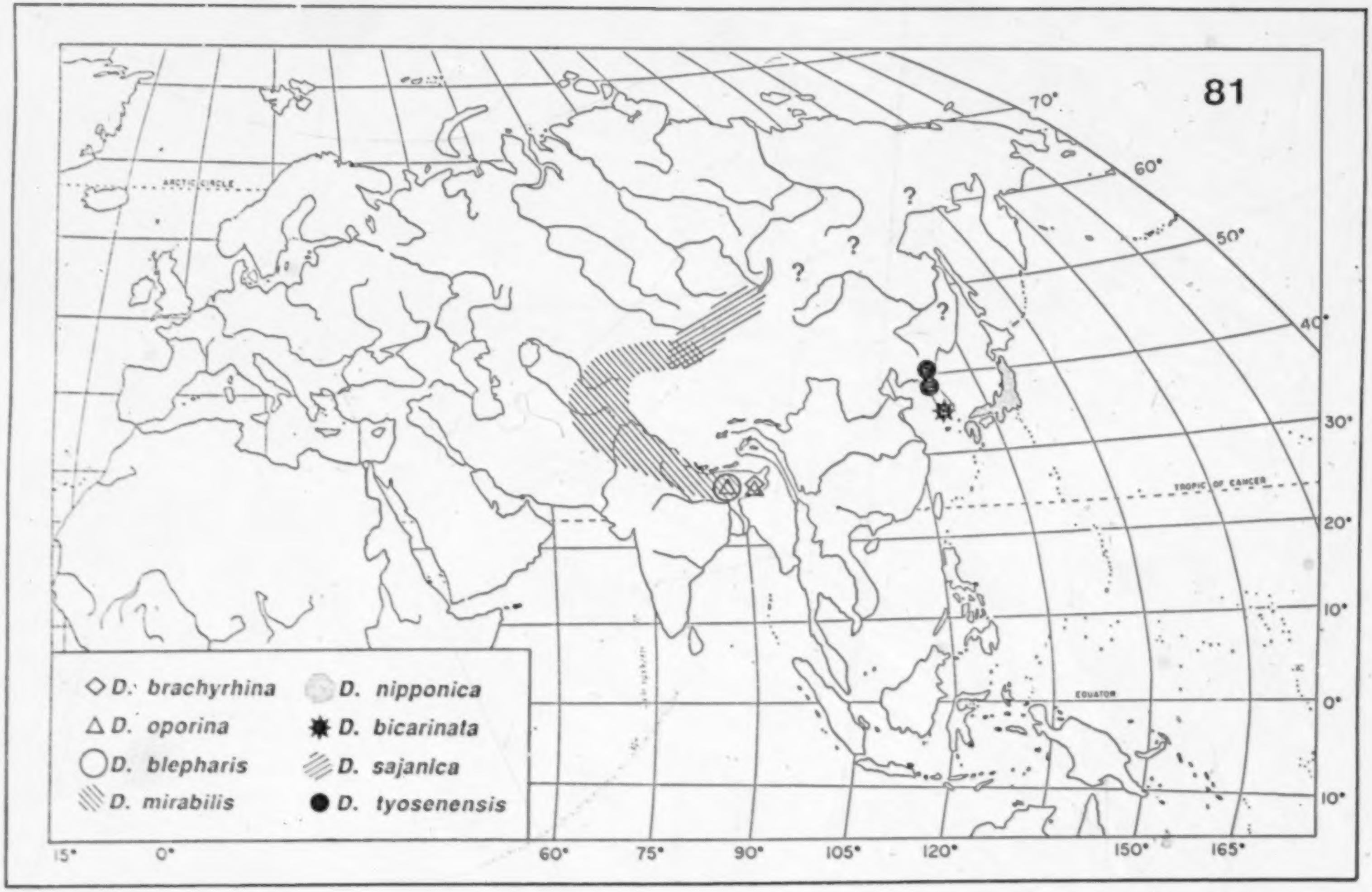
Figure 81. Distribution of Palaearctic species of *Deuterophlebia*.


81
◇ D. brachyrhina
△ D. oporina
○ D. blepharis
▨ D. mirabilis
D. nipponica
✸ D. bicarinata
▨ D. sajanica
● D. tyosenensis
?
?
?
?
ARCTIC CIRCLE
TROPIC OF CANCER
EQUATOR
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40°
30°
20°
10°
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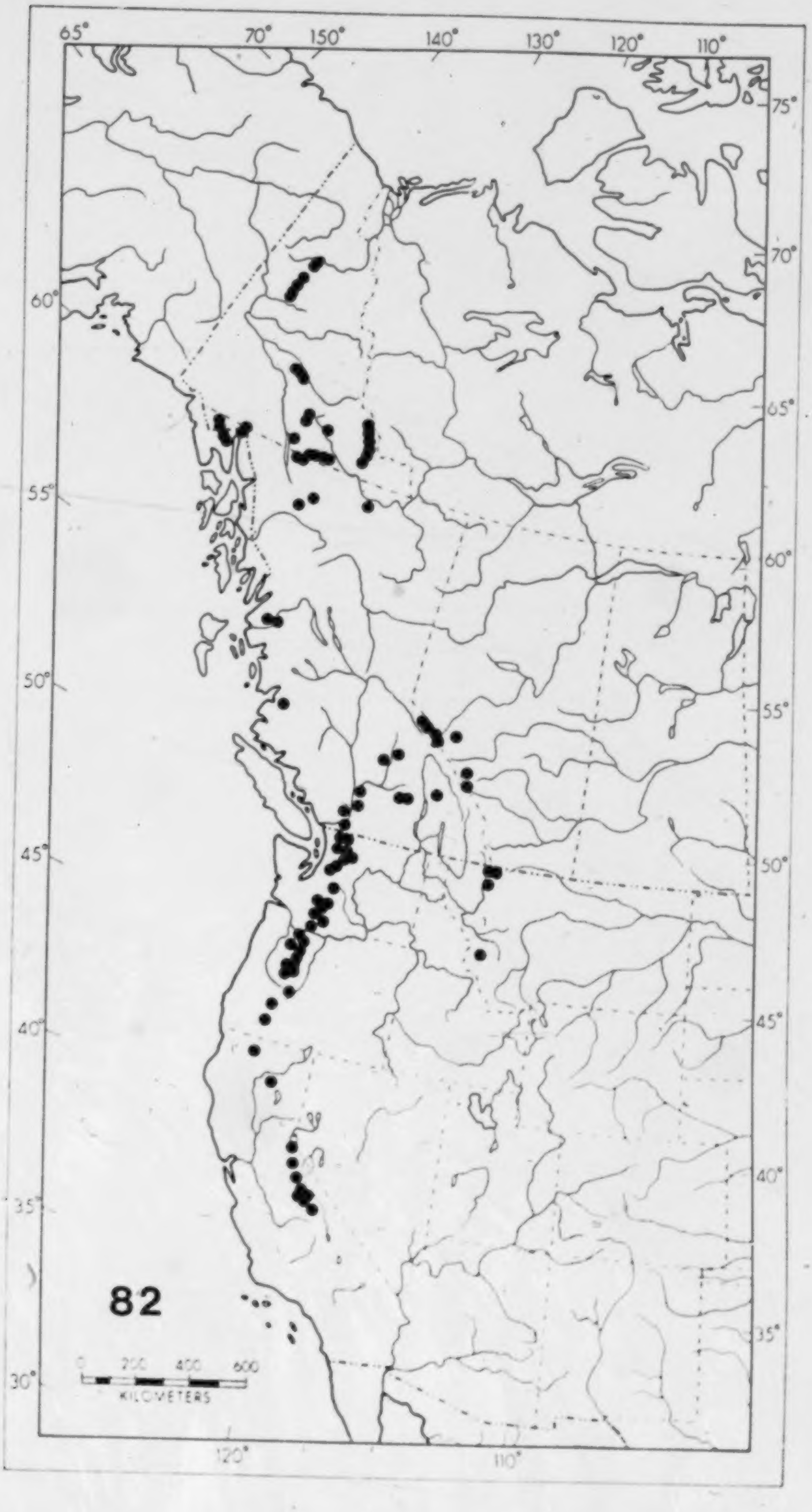
Figure 82. Distribution of *Deuterophlebia inyoensis*.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82

Figure 83. Distribution of *Deuterophlebia shasta* (triangles), *personata* (circles), *vernalis* (stars), and *nielsoni* (squares).

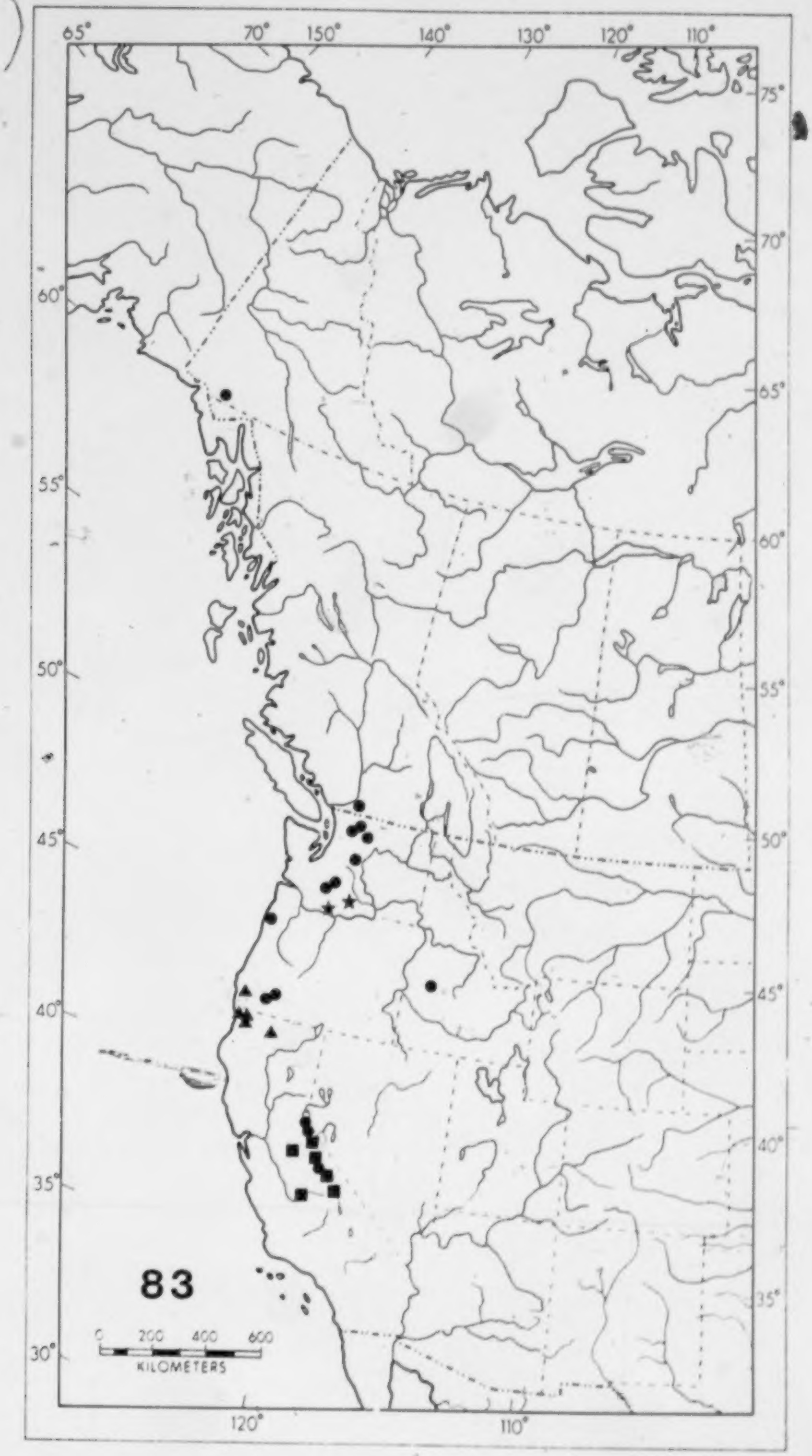

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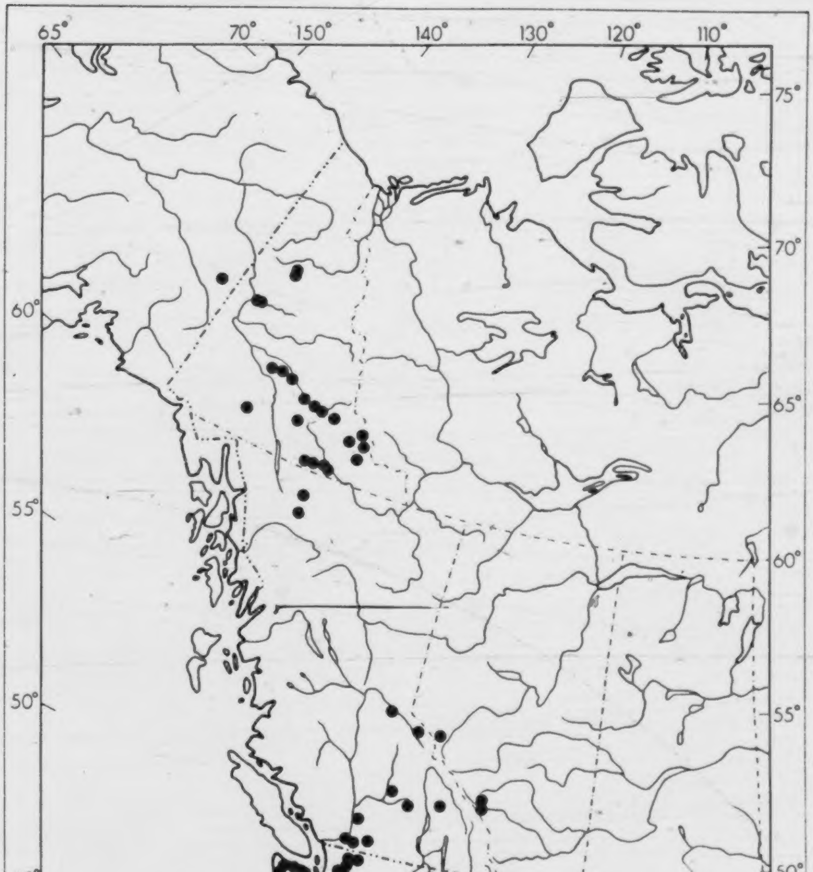
Figure 84. Distribution of *Deuterophlebia coloradensis*.



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KILOMETERS

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5. ECOLOGICAL STUDIES OF NEARCTIC MOUNTAIN MIDGES (DIPTERA: DEUTEROPHLEBIIDAE), WITH EMPHASIS ON HABITAT CHARACTERISTICS, REPRODUCTIVE BIOLOGY AND PHENOLOGIES.

5.1 Synopsis

Mountain midges (Diptera: Deuterophlebiidae) are widespread and seasonally abundant aquatic insects in western North America. Deuterophlebiids are considered stenobionts, requiring cold, high-gradient, mountain streams; however, little is known about the ecology of the group. This study examines the habitat requirements, reproductive biology, and phenologies of Nearctic mountain midges.

Some deuterophlebiids require specific environmental conditions, but most species inhabit a variety of streams. Adult mountain midges show marked diel synchrony, with emergence, flight, and mating during the early morning. Flight behaviour of the short-lived adults is distinct, and includes formation of swarms. Evidence is presented in support of the hypothesis that females shed their wings and actively search for oviposition sites beneath the water.

Asynchronous life histories are typical of Nearctic deuterophlebiids, with egg-hatching and adult emergence extending for 2-3 months. This strategy is adaptive for populations in the Pacific Northwest, where frequent, unpredictable rains can cause flooding, substrate scouring, and high larval mortality. Univoltine life histories were typical of most deuterophlebiids, with only three populations deviating from this pattern. Of the latter, one was predominantly univoltine, but with a small second generation. Another population may be bivoltine, and data for a third are difficult to interpret and could involve sibling species. Temporal isolation of torrenticolous insect populations was apparent, especially among sympatric deuterophlebiids and blephariceids.

5.2 Introduction

Interest in rheophilic, or current-loving, organisms dates back at least to Hora's 1930 monograph about the ecology, bionomics and evolution of the torrential fauna. Although the influence of flowing water on the distribution and abundance of aquatic organisms has always been acknowledged, it is only recently that rheophilic organisms have become a primary subject of benthic research. Much of this interest may be attributed to general reviews (*e.g.*, Vogel 1981; Newbury 1984; Nowell and Jumars 1984), and more specific investigations about larval mayflies (*e.g.*, Soluk and Craig 1988), caddisflies (*e.g.*, Peterson *et al.* 1984; Osborne and Herricks 1987) and black flies (*e.g.*, Craig and Galloway 1987; Eymann 1988) The family Deuterophlebiidae is among these rheophilic specialists, as all life stages are intimately associated with torrenticolous habitats.

Knowledge of the Deuterophlebiidae began more than 60 years ago (Edwards 1922), when male imagos were found in the mountains of Kashmir. Subsequently, Pulikovsky (1924) and Brodsky (1930) reported on larvae and pupae from torrential streams of central Asia. Mountain midges also were found in Japan and Korea (Kitakami 1929; 1938; 1954), India (Singh 1961; Mani 1962; Dubey and Kaul 1971; Kaul 1986), Afghanistan (Tokunaga 1966), Mongolia and northeast Russia (Jedlicka and Halgos 1981, 1985; Jedlicka 1986). At present, eight Palaearctic species of Deuterophlebiidae are known (Edwards 1922; Kitakami 1938; Jedlicka and Halgos 1981; Courtney *in prep*[1]). The first Nearctic records were larvae and pupae from Yellowstone National Park, Wyoming (Muttkowski 1927). Six species have been described from western North America (Pennak 1945; Wirth 1951; Kennedy 1958, 1960; Courtney *in press 2*[1]).

Except for work by Yie (1933) and Kennedy (1958), most published information about deuterophlebiid ecology has been brief mention of habitat or life history, usually in the context of a species description or geographic range extension. Almost nothing is known about the reproductive biology of mountain midges, particularly with regard to mating behaviour and oviposition. Knowledge of deuterophlebiid phenologies is also lacking, partly because of difficulties in effectively sampling for early instar larvae.

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[1] See also chapter 4.

The objective of the present study is to provide detailed descriptions of habitat characteristics and reproductive biology of Nearctic Deuterophlebiidae. Included are data about larval instar determination, and adult emergence times, behaviour, sex ratios, and longevity. Hypotheses about mating and oviposition are also evaluated. Phenological data for deuterophlebiid populations from the Pacific Northwest include information about seasonality, development times, population synchrony, voltinism, and temporal patterns among sympatric deuterophlebiids and other torrenticolous organisms.

5.3 Methods

5.3.1 Collection Techniques. Many of the "standard" collection methods in benthic research are rather ineffective for collecting deuterophlebiids. Although Surber, Hess, or comparable samplers are useful in relatively shallow, gravel-bottom riffles, they are unwieldy and impractical in most deuterophlebiid habitats. General use of this type of sampling device may be a major reason mountain midges are rarely collected in lotic studies. Kick samples are almost as ineffective, because of the tenacity with which deuterophlebiids adhere to the substrate.

Deuterophlebiid larvae are small, typically less than 5mm in length, and in most species, the body is relatively opaque. These factors can influence a collector's ability to see mountain midge larvae on rocks that typically harbour the more noticeable immature stages of black flies, heptageniid mayflies, rhyacophilid caddisflies, and other insects. However, the unusual larval shape and "zig-zag" forward locomotion make deuterophlebiids easy to recognize. Visibility is enhanced by removing the substrate from the stream, allowing the surface to dry slightly, and inspecting the substrate in full sunlight. Substrate color can also influence detection; *e.g.*, species such as *D. inyoensis* Kennedy are more visible on light-colored rocks.

A supplement to direct inspection of substrates, first used by Müller (1895) to collect the psychodid *Maruina* Müller and adopted later for deuterophlebiids by Wirth (1951), involves passing one's hand "slowly and with moderate pressure over the rocks where larvae [occur]" (pg 51, Wirth 1951). Larvae are dislodged from the rock and "cling tightly to the skin", where contrasting body color makes them easily seen. Descriptions of this technique (Wirth 1951; Alexander 1963) implied that the hand should be passed over a rock "in the stream". Although this may result in a few larvae clinging to the hand, most will be lost when the hand is retrieved through the current. The "Müller method" is effective for collecting deuterophlebiids only if the rock has been *removed* from the water. The technique, while sometimes resulting in damaged specimens, is especially useful for collecting the extremely small early-instar larvae. It is also a valuable "final check" after removal of large larvae, or subsequent to rock washes (see below).

The first Nearctic deuterophlebiid was collected in a plankton net (Muttkowski 1927), and colonization by drifting larvae has been reported for Sierra Nevada populations (Kennedy 1955, 1958). Results of the present research suggest that larval drift is infrequent under normal stream conditions, although rapid changes in temperature or current velocity often induced this behaviour in laboratory rearing tanks. Drift nets are useful when objectives are collection of pupal exuviae and emerging adults, and determination of emergence times and sex ratios (see Turner *et al.* 1986).

The most effective method of collecting all larval stages, particularly early instars, is to wash substrates that harbour deuterophlebiids. Rock wash methods were used extensively during this research, and were especially valuable for phenological studies. Procedures included the following steps: (**1**) the rock was removed from a suitable habitat, with hand contact only on the lower surface (*i.e.*, minimizing disturbance of the habitable surface); (**2**) the rock was quickly (< 1 minute) inspected, to determine if deuterophlebiids were present; if larvae or pupae were present, the rock was considered suitable for washing; (**3**) the rock was submersed in a solution of dilute (*ca.* 20%) Ethanol (EtOH), or an EtOH (*ca.* 20%) - Glacial Acetic Acid (*ca.* 5%) mixture; (**4**) all pupae were removed with forceps, following the procedures described below; (**5**) a shaving brush (Camel-hair, or comparable, and preferably with white fibers) was used to brush the rock 5-6 times; (**6**) the rock was quickly rinsed in the solution, to remove larvae that may have been dislodged, but not washed off, by the brush; (**7**) the Müller method (see above) was used as a final check for larvae; (**8**) the brush was examined for larvae that may have become lodged within the fibers; (**9**) the sample solution was poured through a fine-mesh (pore size *ca.* 200μm) fabric / sieve, and all collected material was placed in 95% EtOH; and (**10**) the sample was taken to the laboratory for sorting and enumeration using a dissecting microscope.

By following these steps, qualitative samples of pupae and all larval instars may be gathered. This becomes an effective quantitative method if substrate surface areas are calculated. Rock surface areas for this research were calculated by the following steps: (**1**) exposed (*i.e.* habitable) zones, including top and all lateral surfaces, were determined; (**2**) these zones were partitioned into quadrilateral areas (usually 5-7 per rock, but dependent on rock shape); (**3**) mean width and mean length of each quadrilateral face were multiplied; (**4**) products from the last step were added, to give total rock surface area.

Deuterophlebiid pupae occur on the same substrates as larvae, but most are in small depressions or surface irregularities. Because pupae are firmly attached to the substrate, they are easily damaged by removal. Although pupae may be dislodged with any sharp object (*e.g.*, knife blade, finger-nail), use of a pair of blunt, curved forceps causes the least amount of damage. Pupae should be removed by applying slight downward and inward pressure to the lateral margin of abdominal segments III-V, a region corresponding to pupal attachment discs. Once attachment discs are severed, the pupa can be removed easily.

Adult mountain midges are collected less frequently than immature stages, probably because of temporal factors. The relatively early and sometimes unpredictable emergence times, and extremely short imaginal life, contribute to the paucity of records. If adult collections are desired, a preliminary survey of immature stages is recommended, because presence of mature deuterophlebiid pupae usually indicates a forthcoming adult emergence.

Adult deuterophlebiids are sometimes difficult to see, particularly in situations where flight is immediately over white water, or in sunlit areas far above the stream. Adults, with their large, silvery-blue wings, are most visible when in sunlit areas, particularly if viewed against a dark background (*e.g.*, an opposing, shaded stream bank). Visibility is enhanced by viewing the stream surface from a low angle. Adults over white water habitats may be nearly impossible to see, and collection may require "blindly" sweeping the net over the habitat. At closed-canopy sites, adults may fly in sunlit areas high above the stream (see below), where collection often requires use of a long-handled or telescopic net.

In much of western North America, an alternate method of collecting adult mountain midges relies on the predatory habits of Orb Weaving Spiders (*Tetragnatha* Latreille). Certain species (*e.g.*, *T. elongata* Walckenaer) occur along stream margins, where webs are placed on overhanging vegetation. Webs are often constructed within a half meter of the waters' surface, a height frequented by active deuterophlebiid adults. The delicate midges are entangled easily in webs and, following a large emergence, hundreds of adults may be found on a single web. Depending on weather (*e.g.*, temperature, humidity) and exposure to sunlight, material captured in *Tetragnatha* webs may remain in good condition for several hours. This collection method is advantageous since the collector need not be present during the brief and early emergence period. It also allows collection of samples from several different, and distant, streams on the same date.

5.3.2 Transportation of Live Material. The immature stages of mountain midges can be transported with relative ease. Larvae are best placed on damp filter paper in a loosely sealed container (*e.g.*, petri dish), and transported in a chilled container (*e.g.*, ice-filled cooler). Detached pupae are transported in a similar manner, or left attached to substrates; for the latter, substrates should be covered with moist tissue and placed directly in a chilled container. If the objective is obtaining reared adults, pupae should not be detached from the substrate (see below). Transportation times of up to 30 hours resulted in little mortality (*i.e.*, for *D. inyoensis*, *D. personata* Courtney, *D. vernalis* Courtney, and *D. coloradensis* Pennak); longer transportation times were not attempted.

5.3.3 Laboratory Rearing. Several methods of rearing deuterophlebiids in the laboratory were moderately successful. Artificial streams were constructed from plexiglass tubing, as described by Craig (1977). Air-driven magnetic stirrers were used to generate current velocities ranging from 30-70cm/s (depending on the species being reared). Rearing systems were housed in an incubator at constant temperature (11°C) and daylength (16 hr light / 8 hr dark).

Deuterophlebiids also were maintained successfully in a second type of air-driven system (Lacoursière and Boisvert 1987). Larvae and natural substrates with attached pupae were placed in rearing tanks in which the "sliding plates" (*sensu* Lacoursière and Boisvert *loc. cit.*) had been removed. Current was generated by a laboratory air supply, and the rearing system was maintained in an incubator (*ca.* 10°C).

The most effective method of obtaining reared adults involved collecting rocks with large numbers of attached pupae. Rocks were placed in an incubator, in a loosely sealed plastic container or glass aquarium. A shallow layer of water, of sufficient depth to maintain high humidity but not cover the pupae, was placed in the bottom of the container; this provided enough moisture to prevent dehydration, without reducing the availability of oxygen. Containers were opened at least once per day, to check for emerged mountain midges, replenish the air supply, and pour water over the pupae (to ensure they remained moist). This method eliminates the need for a flowing water, highly-oxygenated system, and circumvents problems of adult damage from flowing water rearing systems (in which adults emerge and attempt to fly, but become trapped in the water and abraded by current).

5.3.4 Phenological Research. During 1986, phenological research was conducted at 17 streams in the Pacific Northwest (Fig. 1). Numbers in Figure 1 refer to the following sites (sites 1-16 in Oregon; site 17 in Washington):

1. Tillamook Co., Cedar Creek (nr confl with Three Rivers), 45°12'N 123°50'W 23m; species present: *D. personata.*
2. Tillamook Co., Nestucca River (ca 3mi above Blaine), 45°15'N 123°39'W 115m; species present: *D. coloradensis.*
3. Yamhill Co., Willamina Creek (ca 6mi above Willamina), 45°08'N 123°29'W 100m; species present: *D. coloradensis.*
4. Benton Co., Marys River (@ Hwy 20 crossing), 44°32'N 123°24'W 85m; species present: *D. coloradensis.*
5. Benton Co., Rock Creek (@ Hwy 34 crossing), 44°30'N 123°26'W 120m; species present: *D. coloradensis.*
6. Benton Co., South Fork Alsea River (@ S Fk Road crossing), 44°20'N 123°32'W 180m; species present: *D. coloradensis.*
7. Benton Co., Crooked Creek (nr confl Ernest Creek), 44°25'N 123°32'W 130m; species present: *D. coloradensis.*
8. Lane Co., Wolf Creek (nr confl Siuslaw River), 43°57'N 123°37'W 105m; species present: *D. coloradensis.*
9. Lane Co., Wildcat Creek (ca 1mi above confl Siuslaw R), 44°00'N 123°38'W 100m; species present: *D. coloradensis.*
10. Josephine Co., Grave Creek (@ Hwy 5 crossing), 42°38'N 123°23'W 325m; species present: *D. personata, D. coloradensis.*
11. Douglas Co., Elk Creek (2.9mi southeast of Tiller), 42°53'N 122°55'W 375m; species present: *D. coloradensis.*
12. Douglas Co., South Umpqua River (2.3mi below Tiller), 42°57'N 122°59'W 285m; species present: *D. coloradensis.*

13. Lane Co., South Fork McKenzie River (nr confl Trail Creek), 44°00'N 122°10'W 620m; species present: *D. coloradensis.*

14. Lane Co., Roaring River (above Roaring River Campground), 45°09'N 122°06'W 295m; species present: *D. inyoensis.*

15. Clackamas Co., Clackamas River (below confl Roaring River), 45°09'N 122°06'W 295m; species present: *D. coloradensis.*

16. Clackamas Co., Roaring River (ca 1km above confl Clackamas River), 45°09'N 122°06'W 295m; species present: *D. inyoensis*, *D. coloradensis.*

17. Klickitat Co., Major Creek (above Hwy 14 crossing), 45°42'N 121°21'W 32m; species present: *D. vernalis.*

These sites represent a diversity of stream types, with regard to geology, physical conditions, and the benthic fauna. Included are streams in the Coast Range (sites 1-9), Klamath Mountains (site 10), Cascade Range (sites 11-16), and Columbia River Gorge (site 17).

Sites were sampled weekly during the activity period of deuterophlebiids, including "negative" samples (*i.e.*, no larvae or pupae found) before and after this period. For each site and date, *ca.* 10 rocks were sampled, following the rock wash and surface area estimation methods described earlier. Resultant calculations included density (number of individuals per square meter (rock surface area)) and percent composition (number of a particular instar / total number of individuals). Data were plotted with the aid of software available for Macintosh™ microcomputers. Temperature data were obtained from minimum / maximum thermometers placed at study sites, or from thermograph records of the United States Geological Survey (Water Resources Division) or Oregon Department of Fish and Wildlife (*i.e.*, Cedar Creek Fish Hatchery).

5.4 Ecology

5.4.1 Habitat. The Deuterophlebiidae are generally considered stenobionts, requiring the cold, clear, rapidly flowing water of alpine streams. Although these features apply to many mountain midge habitats, deuterophlebiids actually occur in a diversity of stream types, ranging from small, clear, closed-canopy creeks, to large, turbid, exposed rivers. Deuterophlebiids apparently can tolerate of a range of pH conditions, as evidenced by collections from acidic, northern brown water streams (*personal observation*; Babcock 1986) to highly alkaline (*i.e.*, with marl-covered substrates) Rocky Mountain sites (*personal observation*). Although mountain midges inhabit a variety of stream types, some species show marked preference for specific environmental conditions, and may be considered stenobionts. Included is *D. inyoensis*, a species generally restricted to small, cold, clear, high-gradient streams. Nonetheless, a few individuals have been found in relatively large, warm rivers. These specimens may have originated in tributary streams, and accidentally colonized larger systems; however, the presence of individuals in larger streams suggests some degree of habitat plasticity. Several species inhabit streams that freeze into the substrate during the winter (*personal observation*; Kennedy 1958, 1960; Babcock 1986). Although apparently tolerant of winter desiccation, Nearctic mountain midges are absent from streams that become dry during summer months.

Deuterophlebiid larvae and pupae typically are restricted to riffle habitats, where substrates are coarse and current velocities high. Most records are from depths of 20-50cm (Yie 1933; Kennedy 1958; Brodsky 1980; Turner, et al. 1986), with comparable values considered by some authors as maximum habitable depths (Kennedy 1981). In fact, larvae and pupae have been collected to depths of at least 1m (*personal observation*), and probably occur in deeper habitats at some sites. Most implied or stated depth restrictions (Kennedy 1981) are probably biased by two factors. Firstly, riffles in small streams are typically quite shallow, relative to similar habitats in larger rivers. A second, and perhaps more important, factor is the difficulty in sampling deep riffles, especially when current velocities exceed 1m/s. Deuterophlebiid larvae and pupae also have been collected in extremely shallow (<5cm), almost madicolous, habitats (*personal observation*). Distributional limits are probably more dependent on substrate, current velocity, or light penetration (*i.e.* in milky, glacial melt-water streams), rather than depth. The role of these factors may also be indirect, via influence on periphyton or dissolved oxygen.

Deuterophlebiid larvae occur on most kinds of hard substrates, including basaltic, granitic and, in some streams, sedimentary rocks. Soft substrates, such as fine sediments, vegetation and wood, are avoided. Kennedy (1958) found that larvae from streams in the Sierra Nevada (California) were abundant on "smooth, light-colored" rocks, but absent from "rough or multicolored rocks such as granite" (pg. 220). He later (Kennedy 1981) made a similar, more general statement. The latter was questioned by Turner *et al.* (1986), who found no preference for light or dark substrates, but noted that larvae were more easily detected on light rocks. I found no rock color preference; however, it is apparent that a "light vs. dark" substrate characterization is too simplistic. Kennedy's qualifying terms "smooth" and "rough" are noteworthy, because substrate texture is probably a more important microhabitat feature than is color. Preferred larval substrates are smooth water-polished surfaces, while sedimentary rocks, and rough granitic or basaltic substrates are avoided at most localities. The immature stages of Blephariceridae, frequent cohabitants with deuterophlebiids, exhibit similar substrate preferences (*personal observation*; Zwick 1977). Larvae of both insect taxa are grazers, feeding on thin periphytic films, but neither occurs on substrates heavily colonized by filamentous algae or moss (*personal observation*; Zwick *loc. cit.*). Unlike the ventral suction discs of larval blepharicerids, deuterophlebiids rely on eversible, crochet-tipped prolegs for attachment and locomotion. Because proleg function is dependent on the presence of some surface irregularities (*i.e.* microscopic roughness), deuterophlebiids are unable to walk on glass or other highly polished surfaces. However, deuterophlebiids also avoid extremely coarse substrates. In both instances, the effect of substrate texture may be indirect, via influences on current (Davis 1986) or periphyton distribution (Reiter 1986).

Although deuterophlebiids typically avoid sedimentary substrates, certain drainages in Oregon's central Coast Range (*e.g.*, Alsea, Siuslaw, and Smith Rivers) provide exceptions to this tendency. Substrates at these sites consist mostly or exclusively (Smith River) of sandstone, and deuterophlebiid larvae and pupae show no apparent preference for basaltic rocks, when available. Interestingly, the unusual tubercled morphotype of *D. coloradensis* (Courtney *in press* 2[1]) occurs only in streams with sedimentary substrates, and tubercle development seems correlated with the amount of this substrate type (*e.g.*, individuals from the Smith River have the most pronounced tubercles). It is possible that these tubercles accrue some hydrodynamic function, perhaps allowing survival on rough sandstone rocks; however, the exact function of these structures remains unknown.

Deuterophlebiids are intimately associated with rapidly-flowing streams, and most published habitat descriptions include some mention of the current regime. Pulikovsky (1924) described the larval habitat as a "swiftly running, clear stream", and stated that larvae "occurred only where the current was very rapid" (pg. 46). Many subsequent publications included velocity measurements (Brodsky 1930; Yie 1933; Kennedy 1958; and others), with most ranging from 1.0-1.5m/s, and 0.5m/s (Kennedy 1958) and 3-4m/s (Brodsky 1980) representing published minimum and maximum values, respectively. Current velocity data from the present investigation show comparable overall values (0.2-2.0m/s)[2], and suggest current regime preferences by certain taxa. The latter was evident in populations of *D. inyoensis* from the Sierra Nevada and Cascade Range, where individuals were abundant in velocities of 1.5-2.0m/s, but rare when flow was <1.0m/s. Flow restrictions seem to disappear with increasing latitude, as most populations of *D. inyoensis* from the Yukon Territory were found in lower current velocities (to *ca.* 0.5m/s). Possible explanations of latitudinal differences may relate to thermal conditions, levels of dissolved oxygen, or other physical parameters. Although other species (*e.g.*, *D. coloradensis*) occurred in a wide range of flow (0.2-1.5m/s), densities were usually highest in velocities of 0.5-1.0m/s.

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[1] See also chapter 4.

[2] Velocities were measured with a PVM-2™ (Montedero Whitney, Inc.) flowmeter.

Pupae are found in the same microhabitat as larvae, usually within small cracks or depressions on rock surfaces. Pupae occur on the top and lateral surfaces of rocks (*personal observation*; Turner, *et al.* 1986), or may exhibit preference for the top surface (Kennedy 1958). The lateral profile of the dorsoventrally flattened deuterophlebiid pupa is rather streamlined, and it is tempting to assume that pupae orient to the current (*i.e.*, as in Blephariceridae), with the thoracic region positioned upstream. However, there appears to be no correlation between pupal orientation and current direction or velocity. Pupae evidently prefer darker substrates at some sites (Kennedy 1958); however, this is not a general trend in all streams (*personal observation*). Some data suggest that pupae are most abundant near the splash zone, in shallower habitats than larvae (Kennedy 1958). Occasional discovery of dead, un-emerged pupae on emergent substrates (*personal observation*) would seem to support this theory; these individuals presumably pupated on submerged substrates, when water levels were higher. In spite of this trend for some populations, pupal distribution is essentially uniform (*re.* depth) at most sites.

Stream temperatures appear to have a major influence on both the distribution and phenology of deuterophlebiids. Most species inhabit relatively eurythermal streams that range from 0°C in winter, to >20°C in summer; however, the thermal "activity window" for larvae and pupae is considerably narrower. In general, eggs begin hatching when temperatures reach 6-8°C, with most development between 10-15°C, and declining activity as temperatures approach 20°C. This pattern was seen in populations of *D. coloradensis*, *D. vernalis*, and *D. personata*, and *D. shasta*. Last-instar larvae or pupae were occasionally found in streams warmer than 20°C, but such temperatures are probably near the lethal maximum for most individuals. The stenobiontic species, *D. inyoensis*, is active at cooler temperatures, and has a rather narrow thermal range (most records 5-10°C).

5.4.2 Instar Determination. As in most Nematocera, deuterophlebiids pass through four larval instars. Structural features used to separate instars have included total body length (Pulikovsky 1924, Brodsky 1930, Yie 1933), head capsule width (Pulikovsky 1924, Brodsky 1930, Kennedy 1958), number of proleg crochet rows (Pulikovsky 1924, Kitakami 1938), and proportions of antennal articles (Kitakami 1938). Estimates of instar number have ranged from three (Pulikovsky 1924) to five (Yie 1933), with four the most common prediction (Brodsky 1930, Kitakami 1938, Kennedy 1958). Among the latter publications, only Kitakami and Kennedy included data for first instar larvae. Brodsky (1930), like many early workers, relied primarily on total body length, a feature which shows considerable overlap across instars (see below).

Instar characteristics were determined for all Nearctic species except *D. nielsoni* Kennedy. Data for head capsule width, and head capsule width *vs.* total length, confirm the presence of four larval instars in *D. inyoensis* (Fig. 2), *D. shasta* Wirth (Fig. 3), *D. personata* (Fig. 4), *D. vernalis* (Fig. 5), and *D. coloradensis* (Figs. 6, 7). Head capsule width is one of the most reliable features for distinguishing instars (*cf.* Figs. 2a-7a), while total length shows considerable overlap between instars (*cf.* Figs. 2b-7b). Number of proleg crochet rows can also be diagnostic of a particular instar; depending on the species, number of crochet rows are: instar I (1); instar II (3 or 4); instar III (5-9); instar IV (7-14). Relative development of cranial sclerites and antennal article proportions can also assist separation of instars (Courtney *in press 1*, *in press 2*).

5.4.3 Adult Emergence. Eclosion from the pupal case requires that the pupa be firmly attached to the substrate. Thoracic sutures are ruptured by downward pressure from legs and wings, and the emerging adult apparently reaches the stream surface in an air bubble (similar to the Blephariceridae). Laboratory observations suggest that adult males are incapable of pulling themselves out of the pupal case, and must rely on assistance from the current and/or an air bubble for successful eclosion. In contrast, females readily emerge without the aid of current. This difference undoubtedly reflects sexual dimorphism, especially *re*. the acropod (*cf*. Figs. 4.55, 4.66). The male acropod has a markedly expanded empodium and vestigial tarsal claws, the latter of which makes males incapable of terrestrial locomotion (*e.g.*, walking out of the pupal case).

5.4.4 Flight Behaviour and Swarming. I observed deuterophlebiid flight behaviour for more than 50 populations, with most data for the widespread species *D. coloradensis* and *D. inyoensis*.

Adult mountain midge activity is characterized by pronounced diel synchrony, with emergence, flight, and mating occurring for a brief period in the early morning. The largest emergences, and most observations of flight behaviour, occurred under clear skies; however, comparable behaviour was demonstrated during inclement weather. Depending on the species, emergence times were between 0700-0900h, with flight restricted to approximately 2-3 hours. In most populations, there was a peak flight period of 30-45 minutes. During their aerial life, deuterophlebiids exhibit characteristic and sexually distinct flight behaviour (Fig. 8), with adult males typically coursing back and forth in a zig-zag, upstream-directed, flight path. Males may form loose aggregations that move upstream as a relatively coherent unit, and these groups sometimes form stationary swarms. The zig-zag flight persists within swarms, but a third dimension (*i.e.*, height) enters the behavior. Female mountain midges exhibit a distinctly different behaviour, typically flying in an essentially straight path and at relatively greater heights than males. The height of female flight often approximates the tops of male swarms, which could enhance the females' ability to locate swarms and potential mates.

The magnitude of adult emergence appears to influence behaviour, as stationary swarms form primarily when large numbers of adults are present. Wind may also affect flight behaviour and swarm formation. Stationary swarms typically occur over whitewater riffles or emergent, mid-stream boulders. Although these features may serve as swarm markers, sunlight appears to be the most important determinant of swarm location, at least in certain species or populations. This is particularly true of deuterophlebiids inhabiting small, closed-canopy streams (*e.g.*, many *D. inyoensis* populations).

Table 1 presents a partial summary of swarm data for several Nearctic species, with most pertaining to *D. coloradensis* and *D. inyoensis*. Data show that *D. coloradensis* typically swarms near the water surface. The one exception (Deadwood River, Idaho) represents a site where habitats consist almost exclusively of whitewater rapids. At this site, all observed adults were 5-8m above the stream, perhaps because flight at the "usual" height of 0-1m would result in substantial mortality. These data suggest that, although *D. coloradensis* adults generally fly nearer to the water than other species, swarm height may be relatively plastic. Data for *D. inyoensis* suggest a strong correlation between canopy cover and swarm height. Wahkeena Creek, in the Columbia River Gorge, is listed, even though adults have been neither collected nor seen at the site. The stream contains high densities of larvae and pupae, and observations of adult emergences were attempted on numerous occasions; however, adults were never evident (even in instances when mature pupae were abundant, and adults presumably emerging). Wahkeena Creek remains shaded during the [expected] morning emergence period, and the nearest sunlit areas are in the treetops. If, as suggested by other *D. inyoensis* data, sunlight is an important determinant of swarm location, Wahkeena Creek mountain midges may be swarming near the treetops, high above the stream.

5.4.5 Mating Behaviour. Female adults were seen entering swarms on several occasions; however, tracing their path any further proved impossible. Mating has not been observed, though presumably it occurs in flight, and within swarms. Indirect support for this hypothesis comes from the fact that males are incapable of terrestrial locomotion (see above), and mating pairs are not found on emergent substrates or streamside vegetation. Direct evidence of aerial mating comes from collection of a pair of *in copula D. coloradensis* from an adult swarm. Out of thousands of adults that I collected (of all

Nearctic species), this was the first and only mating pair discovered; this statistic suggests further that copulation is quite rapid.

5.4.6 Adult longevity. A parameter related to flight and swarming is adult longevity. The imaginal mouth is represented by a simple oral opening, with no evidence of functional mouthparts (*cf.* Figs. 4.55-4.57). Aphagia in adults is indicated by the vestigial digestive tract, which consists of shrivelled remnants of pre-rectal elements, with no anal opening. Inability to feed, coupled with the active aerial existence, undoubtedly contributes to the brief adult life.

Additional insights into adult longevity come from field and laboratory observations. The appearance of moribund males on backwater surfaces signified the end of the flight period at many sites; this typically occured *ca.* two hours after the first adults emerged. Adult males collected from swarms did not survive beyond the two hour flight period, even if placed in an ice-filled cooler. Live female adults were sometimes discovered on spider webs (of *T. elongata*) as late as noon, and on two occasions, both cool, cloudy days, live males were found on webs long after the emergence period (as late as 1445h). Otherwise, live adults were not found on emergent subtrates or streamside vegetation after the flight period. Laboratory observations were based on rocks with attached pupae, reared by methods described earlier (5.3.3). Few reared males were capable of complete eclosion, with most able to pull the head, thorax and abdomen out of the pupal exuviae, but not the wings and antennae. The longevity of these "grounded" individuals was substantially longer than under field conditions, with some surviving for 30 hours, and one for almost 40 hours. Reared females also survived several hours past the normal flight period, during which time they often oviposited (even though unmated) in the rearing tank; however, no females survived more than 24 hours.

Observations of adult structure and behaviour suggest the following: (**1**) Male adults lead a strictly aerial life, with the metabolic costs of continuous flight resulting in a longevity of about two hours. (**2**) Females adults spend relatively less time in flight, and longevity is dependent primarily on time needed for oviposition. Females probably fly briefly, mate once, and spend most of their life searching for oviposition sites (see below). (3) No adults (including ovipositing females) survive beyond, nor participate in, more than one flight period. Furthermore, females lose their wings during oviposition activities (see below), precluding involvement in subsequent flight periods.

5.4.7 Oviposition. Oviposition has not been observed in the field, though two major hypotheses exist: (**1**) *Broadcast* oviposition, with the female either dipping the abdomen into the water to release eggs (from emergent substrates or while in flight), or simply falling into the stream, and releasing eggs while drifting downstream. The end result is that the eggs reach the substrate passively, settling wherever the current dictates. (**2**) *Active*, beneath-water oviposition, with the female landing on emergent substrates, re-entering the stream, and actively searching for oviposition sites.

Near the end of the flight period, wingless females are often found on the surfaces of backwaters (in fact, *winged* females are uncommon in these samples); however, this observation may fit either oviposition theory. Females of *D. nielsoni* apparently have been found "with eggs scattered all over the abdomen ... on [emergent] rocks in the stream" (Kennedy 1958, pg. 223), suggesting broadcast oviposition from emergent substrates.

My data support the alternate hypothesis, beneath-water oviposition. Among the more convincing evidence is the occasional discovery of wingless females on submerged rocks, several hours after the flight period. These individuals, which invariably contained a partial compliment of eggs, were found on the same substrates as larvae and pupae. Other support for beneath-water oviposition comes from laboratory observations. Females reared from larvae in artificial streams (see 5.3.3) were sometimes found on substrates in the rearing system; all were wingless, having had shed the wings at the water surface, and all were able to crawl over the substrate, even against curent velocities of 50cm/s. Most females reared by other methods (*e.g.*, from pupae attached to rocks) were placed in a dish containing water and partially emergent rocks, in order to observe oviposition behaviour (even though females had not mated). All females that oviposited, did so beneath the water, on substrates provided.

Deuterophlebiid females produce very few eggs, typically only *ca*. 100-150. In light of this low fecundity, careful selection of oviposition sites would seem adaptive. Because of the short imaginal life, pharate adults with fully-developed eggs can be dissected from pupae, allowing easy and accurate estimates of fecundity. Estimated fecundity varied substantially both between and within Nearctic species (*cf*. Fig. 9a-e); however, in most species, there was a strong correlation between fecundity and pupal size.

5.4.8 Phenological Research. Phenological data are presented for Nearctic species of *Deuterophlebia*. Information about some species is based mostly on publications (*e.g.*, *D. nielsoni*) or qualitative observations (*e.g.*, *D. shasta*). However, quantitative data for populations in the Pacific Northwest are the focus of discussion. Particular emphasis is on representative populations of *D. personata* (Cedar Creek), *D. inyoensis* (Roaring River (Lane Co.)), *D. vernalis* (Major Creek), and three populations of *D. coloradensis* (one from the Coast Range (South Fork Alsea River) and two from the Cascade Range (South Fork McKenzie and Clackamas Rivers)). Data for other sites are given in Appendix B.

5.4.8.1 Results. Data for Cedar Creek *D. personata* (Fig. 10) are typical of most populations of this species. Hatching of eggs began in late February, when stream temperatures started to warm (*i.e.*, regularly exceeding 7-8°C). The first pupation occurred in late March, and first adult emergence in mid April. As at other sites, most of the year was passed in the egg stage. Data suggest a univoltine life history, with protracted hatching and emergence. Proportional data (Fig. 10b) show moderately good developmental "progression" of life stages, and suggest a single, asynchronous generation. Qualitative data indicate that other *D. personata* populations follow a similar pattern, except that the activity period is generally later in the year (*e.g.*, mid summer for populations in the North Cascade Range of Washington).

Data for the South Fork Alsea River (Fig. 11) are similar to those of most Coast Range populations of *D. coloradensis* (*cf.* Figs. B.1-B.7). Egg-hatching began when stream temperatures regularly approached 9-10°C, in late February. The first pupa was collected in early April, and first adults evident in late April. As in *D. personata*, data suggest a univoltine life history, with protracted hatching and emergence. Cascade Range *D. coloradensis* populations showed comparable phenologies, except that the larva to adult activity season typically started 1-2 months later than at coastal sites. At the South Fork McKenzie River (Fig. 12), eggs began hatching in mid April, when snowmelt runoff had diminished and stream temperatures started to increase. Pupae were first seen in late May, and adults near the end of June.

The above phenologies (*i.e.*, characterized by asynchronous and univoltine life histories) were typical of most populations examined during this research (*cf.* Figs. B.1-B.8). However, populations from Roaring River (Lane Co.), Clackamas River, and Major Creek apparently do not fit this pattern. Roaring River, in the McKenzie River watershed of the Cascade Range, is a noticeably stenothermal system, with weekly temperature ranges rarely exceeding 2°C and the entire seasonal (March to October) range only 2-8°C. The site contains *D. inyoensis*, a typical inhabitant of torrenticolous, alpine streams. Most *D. inyoensis* populations have a brief, synchronous activity period, and univoltine life history (*personal observation*; Kennedy 1960). Consequently, data for Roaring River (Fig. 13) were unexpected. Although data generally support a univoltine hypothesis, a minor hatching peak in late August suggests a small, second generation. The population showed extreme asynchrony of hatching (16 weeks), and markedly protracted development times, with the first adults emerging in early June, 12 weeks after eggs began hatching.

In terms of physical and faunal characteristics, the Clackamas River seems identical to most Cascade streams (*e.g.*, South Fork McKenzie River). In spite of this apparent similarity, the deuterophlebiid phenology was markedly different (Fig. 14). Data suggest 2-3 generations, but peaks are not sharply separated, with hatching of eggs essentially continuous (23 weeks). In addition, the developmental progression of larval instar I to pupae typical of other sites (*cf.* Fig. 12a), was not evident at the Clackamas River.

Major Creek, one of only two streams containing *D. vernalis* (Courtney *in press 2*) is in the arid, eastern end of the Columbia River Gorge. The site is characterized by relatively harsh physical conditions, including winter temperatures near 0°C, occasional spring floods and, during the summer, temperatures to 30°C, with markedly decreased stream flow. Physical conditions require that deuterophlebiid larvae and pupae are active for only 2-3 months, which may explain the relatively synchronous phenology (Fig.15). Interestingly, the population appears to have a bivoltine life history. The presence of two generations is suggested further by the second hatching peak coinciding with the first appearance of adults, in mid April. With the exception of pupal data, there is good developmental progression of life stages. Proportional data show two significant peaks (with 95% confidence[1]) for all larval instars. Although pupal data show two peaks, they are not significantly different; the latter may reflect greater longevity of the pupal stage, relative to individual larval instars.

5.4.8.2 Comparative phenologies of Nearctic species. Development times for Nearctic deuterophlebiids are summarized in Table 2. Information about Sierra Nevada (California) populations of *D. inyoensis* and *D. nielsoni* are from papers by Kennedy (1960 and 1958, respectively), whereas data for other species are from personal observations or the present analysis. Kennedy's 1958 paper was a landmark publication in many ways; however, many of his phenological conclusions probably were incorrect. Kennedy suggested that *D. nielsoni* was trivoltine, and that each generation (particularly the first) was very synchronous. A major problem with this prediction is that *D. nielsoni* (*sensu* Kennedy) actually includes two species (Courtney *in press 2*). Furthermore, Kennedy's sampling methods were not rigorous, consisting of enumeration of larvae and pupae *in situ*. Because of the minute size of instars I and II, this method may have led to inaccurate estimates of relative abundance. In fact, only six instar I larvae were collected during Kennedy's study. A 1985 visit to Kennedy's study site verified the presence of pupae and all larval instars, at a time (mid July) corresponding to the middle of the "synchronous" first generation (*sensu* Kennedy). Although year-to-year differences may explain some phenological variation, data for other populations suggest development never approaches the synchrony predicted by Kennedy. Other of Kennedy's predictions (*e.g.*, duration of pupal stage) seem reasonable, but suggest substantial differences between *D. nielsoni* and most species. Discrepancies could, however, reflect differing thermal regimes at study sites.

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[1] Calculated from "Table 23 Confidence limits for percentages" (Rohlf and Sokal 1981, pp156-162).

Kennedy's (1960) conclusions about *D. inyoensis* phenologies were based solely on collection of pupae and instar IV larvae. I consider his predictions rather dubious, since elucidation of phenologies should include examination of early instars. Data for most Sierra Nevada *D. inyoensis* populations show little evidence of the highly synchronous pattern suggested by Kennedy, and instead, fit the pattern labelled as "Typical" in Table 2 (*personal observation*). Again, however, there can be significant differences between sites (*cf.* "Typical" and Roaring River data, Table 2).

5.4.8.3 Summary of phenological research. The focus of this research was to provide information about seasonality, development times, population synchrony, and voltinism of Nearctic species of *Deuterophlebia*. Mountain midge populations from the Pacific Northwest demonstrate, to a great extent, rather similar life histories. Seasonal timing of egg hatching is probably dependent on thermal cues, though other stimuli (*e.g.*, photoperiod) may also be involved. At most sites, activity (*i.e.* hatching of eggs) began when stream temperatures increased from their typical winter levels (0-5°C) to *ca.* 7-8°C.

Development time ranged from 5 to 12 weeks, and showed considerable variation between, and sometimes within, species. Different thermal regimes probably account for most variation, and may explain lack of agreement with published data (*e.g.*, Kennedy 1958). Although thermal data have not been compiled for all sites, streams for which data are known suggest that cooler temperatures are responsible for longer development times, relative to published values.

Asynchronous hatching, development, and emergence is typical of deuterophlebiid populations in western North America. This is adaptive for western streams, where frequent, unpredictable floods can cause extensive substrate scouring and correspondingly high mortality of immature stages. Asynchronous life histories are a mechanism by which deuterophlebiids may overcome the potentially devastating effects of such events.

This research has demonstrated that most deuterophlebiid populations are univoltine, at least in the Pacific Northwest. This pattern was evident for all coastal and most Cascade Range streams. Data for only one population, *D. vernalis* from Major Creek, suggest a bivoltine pattern. Voltinism plasticity, perhaps reflecting unique environmental conditions, was demonstrated by the *D. inyoensis* population from Roaring River (Lane Co.). Lastly, the Clackamas River *D. coloradensis* population provided inconclusive data. If these data reflect the phenology of a single species, up to three generations may be completed in a single season; however, extreme asynchrony makes distinguishing cohorts a formidable task. Alternatively, sibling species may be involved. Certain of the area's black flies (Simuliidae) are known for their diversity of isomorphic cytospecies (Newman 1983). If the same is true of the deuterophlebiid fauna, resolving the Clackamas River phenology may require cytogenetic or biochemical studies.

5.4.9 Reproductive Isolation of Sympatric Taxa. Reproductive isolation of sympatric deuterophlebiids and other torrenticolous insects was evident in many western streams, and usually included some type of temporal separation. This discussion focuses on isolation of sympatric species of *Deuterophlebia*, and sympatric Deuterophlebiidae and Blephariceridae, both of which are dipteran grazers found in similar microhabitats.

5.4.9.1 Sympatric species of *Deuterophlebia*. Among Nearctic species, the most common sympatric combination is *D. inyoensis* and *D. coloradensis*. The typical pattern of distribution for these species (Fig. 16) has *D. inyoensis* active early and mostly in upstream reaches. As the season progresses and temperatures increase, *D. coloradensis* begin hatching in downstream reaches. Both taxa may overlap temporally in mid-reaches, but because of slight differences in life history (*i.e.*, semaphoronts non-overlapping) and microhabitat preference, competition for resources should be minimal. This scenario, although based primarily on qualitative data, seems to apply for most streams.

Other forms of reproductive isolation are indicated in Table 3. The term "reproductive" isolation is used somewhat loosely, since certain data refer to immature, rather than reprod[illegible]tive, stages. "Habitat" refers to spatial (current regime) separation at a particular point in time (*i.e.* assumes temporal overlap), and "Temporal" categories includes the interrelated parameters, temperature and season. Most sympatric combinations include either *D. inyoensis* or *D. coloradensis*, with these species generally active "early" and "late", respectively. One of the most interesting combinations involves *D. inyoensis*, *D. personata* and *D. coloradensis*. As discussed elsewhere (Courtney *in press 2*), these species coexist in certain streams in the Cascade Range of Washington and southern British Columbia. At all sites, the activity period of *D. personata* falls between, but broadly overlaps, those of the other two species. However, reproductive isolation of *D. personata* is probably absolute, since populations appear to be parthenogenetic.

5.4.9.2 Sympatric Deuterophlebiidae and Blephariceridae. Mountain midges coexist with other torrenticolous organisms, including several species of another dipteran grazer, the Blephariceridae. Data for some localities (*e.g.*, Willamina Creek, Fig. 18a) suggest temporal isolation may be acting to diminish competitive interactions of deuterophlebiids and blephariceridae. The following temporal sequence is typical of many coastal streams: *Agathon comstocki* (Kellogg) active early, followed by *D. coloradensis*, then *Blepharicera ostensackeni* Kellogg. This may suggest some kind of competitive interaction, with food or perhaps space representing a limiting resource. Mouthpart structure and observed feeding behaviour (Courtney *in press 1*) indicate that the degree of food overlap may not be as great as previously thought. While larvae of both families are grazers, blephariceridsare essentially "scrapers" (*sensu* Lamberti *et al.* 1987), feeding primarily on adnate elements of the periphyton, and deuterophlebiids are "browsers" (*sensu* Lamberti *et al. loc. cit.*) of the periphytic "canopy". This distinction may seem trivial, but could explain the almost complete phenological overlap at other sites (*e.g.*, most Cascade Range streams).

Data for the Nestucca River (Fig. 18b), a coastal site with only one species of blepharicerid (*A. comstocki*), demonstrate that the deuterophlebiid activity period is rather protracted, relative to Willamina Creek. This may suggest that the extended activity period of Nestucca River deuterophlebiids reflects the absence of *B. ostensackeni*. Another consideration is the potential role of black flies, since decreasing deuterophlebiid abundance was generally coincident with increasing simuliid abundance. Thus, competition for space with black fly larvae may help shape deuterophlebiid phenologies. Research on streams in southern California has demonstrated aggressive interactions between larval simuliids and blepharicerids, with the latter being competitively displaced (Dudley 1985, *personal communication*[1]). Similar interactions may occur between black flies and deuterophlebiids.

The applicability of these competition scenarios is challenged by examining data for other sites. Data for Wolf Creek, a site where blepharicerids are absent and black flies scarce, are plotted in Figure 18c. In spite of the lack of these potential competitors, the deuterophlebiid phenology is essentially identical to those of sites with these groups. This suggests that temporal patterns in mountain midges may simply be an artifact of some other parameter (*e.g.*, temperature). In fact, deuterophlebiid populations typically showed decreasing densities as temperatures approached 20°C. Furthermore, thermal effects may be indirect, *via* dissolved O_2, food resources, or some other variable. Certainly, many different influences (including biotic, abiotic and historical effects) have contributed to the life history characteristics of mountain midges.

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[1] "Competition between dissimilar stream insects" — paper presented at the 33rd annual meeting of the North American Benthological Society, Corvallis, Oregon [June 25-28].

5.5 Conclusions

Mountain midges are widespread and seasonally abundant aquatic insects in western North America. Although some species are stenobiontic, most inhabit a variety of streams, ranging from cold, high-gradient, mountain streams to relatively warm, lowland rivers. However, all species are restricted to riffle habitats with high current velocities. Adult mountain midges exhibit marked diel synchrony, with emergence, flight, and mating during only a few hours in the early morning. Flight behaviour of the short-lived adults is distinct, and typically includes formation of male swarms. Subsequent to probable aerial mating, females shed their wings and actively oviposit beneath the water.

In spite of the short life and pronounced diel synchrony of adult deuterophlebiids, the prevalent *modus vivendi* includes asynchronous hatching, development and emergence. This may seem counter-adaptive for an ephemeral insect with relatively low fecundity; however, "spreading the risk" may in fact be the best strategy for torrenticolous habitats. These habitats may experience frequent and unpredictable floods, with concomitant substrate scouring and high mortality of benthic organisms. Asynchronous life histories are a mechanism by which these organisms may overcome the potentially devastating effects of such events.

Reproductive isolation of sympatric Deuterophlebiidae, Blephariceridae, and other torrenticolous organisms, was evident in many Nearctic streams. Determining the exact mechanism for these patterns was beyond the scope of the present investigation, but several hypotheses were generated, including competition for food and/or space, and the influence of certain environmental parameters. It is hoped that this research has provided the impetus and framework for future studies about the ecology of deuterophlebiids and other torrenticolous organisms.

Table 1. Data for selected observations of swarming in Nearctic species of Deuterophlebiidae. Canopy cover is a relative measure of stream shading, from 0 (fully exposed) to 5 (closed canopy); Size = number of males in swarms.

Species	Site	Canopy cover	Swarm Data			
			Time (hr)	Location	Height (m)	Size
D. inyoensis	Bensen Ck (Yukon)	0	0800-0820	riffle (cldy)	0-1.5	5-10
	Glacier Ck (California)	1	<0800-0930	sunlit riffles	0-3	50
	Roaring R (Oregon)	3	0830-0915	sunlit areas	5-6	25
	Lost Ck (Washington)	4	0745-0900+	sunlit areas	>15	50
	Wahkeena Ck (Oregon)	5	??	sunlit treetops?	30+?	??
D. shasta	Smith R (California)	0	<0900-0945	sunlit rapid/boulder	1-10	>1000
D. personata	Grass Lake Ck (California	4	0915-0945+	waterfall	3-4	25
	Cedar Ck (Oregon)	3	0800-0845	rapid (cldy)	0-1	5-10
	Panther Ck (Washington)*	3	0915-0945	-	2-5	-
D. vernalis	Major Ck (Oregon)	0-2	0800-1000	riffles (cldy)	0-1	5-10
D. coloradensis	McGee Ck (California)	1	0830-1015+	riffles (cldy)	0-1	50
	Oregon (several sites)	0-2	0745-1000	sunlit riffles	0-1	50-100
	Clatskanie R (Oregon)	2	0745-0930	sunlit areas**	0-1	50-100
	Colorado (several sites)	0-2	0830-1100	sunlit riffles	0-1	>10,000
	Yukon (several sites)	0	0800-0900	sunlit riffles	0	10-15
	Deadwood R (Idaho)	0	1000-1100	sunlit rapid	5-8	25-50

* females only (parthenogenetic population); ** swarms over both riffles and pools

Table 2. Summary of development times for Nearctic species of Deuterophlebiidae. Data in weeks, unless otherwise stated.

Species	Site	Duration of Egg Hatching	Larval Stage	Pupal Stage	First Adult (Σ Devel.)	"Cohort" Emergence	Population Activity	Source of Data
D. inyoensis	Sierra Nevada	??	11 days	11 days	22 days	5 days	29 days	Kennedy 1960
	"Typical"	5	4-5	3-4	8	4	12	This research
	Roaring R	16*	7*	5*	12*	ca. 12*	27+	This research
D. personata	Cedar Ck	6	4	3	7	9	15	This research
D. shasta	Smith R	10+?	??	??	??	??	16+?	This research
D. vernalis	Major Ck	4*	2-3*	2*	5*	3-4*	10	This research
D. nielsoni	Sierra Nevada	1 day*	10 days*	9 days*	19 days*	1 day*	ca. 9	Kennedy 1958
D. coloradensis	"Typical"	10-15	4-5	2-3	8-9	10	15-20	This research
	Clackamas R	23	5-7	3	11	17+	27	This research

* refers to first generation

Table 3. Generalized patterns of reproductive isolation in sympatric species of Nearctic Deuterophlebiidae; empty boxes refer to overlapping characteristics.

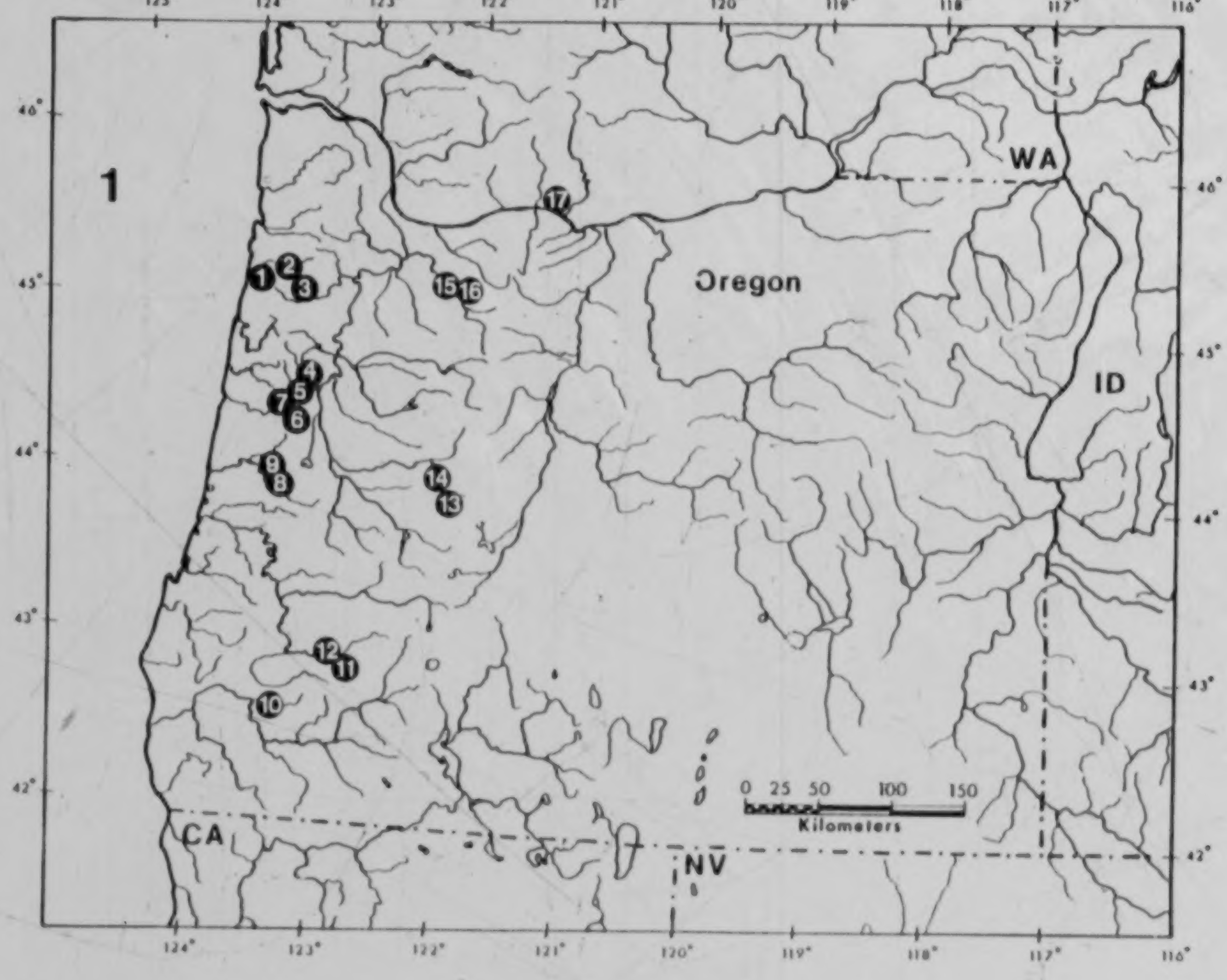
SYMPATRIC SPECIES	HABITAT	BEHAVIOURAL	TEMPORAL	
	Current regime	Swarm Height	Thermal regime	Seasonal activity
D. inyoensis *D. coloradensis*	Rapid Slow	High Low	Low High	Early Late
D. inyoensis *D. personata** *D. coloradensis*	Rapid Intermediate Slow	High - Low	Low Low-High High	Early Mid Late
D. inyoensis *D. shasta*		High Low-High		Early Late
*D. personata** *D. coloradensis*			Low High	Early Late

* parthenogenetic populations

Figure 1. Map showing sampling localities for phenological research.

Sample sites:

1, Tillamook Co., Cedar Creek; species present: *D. personata.*
2, Tillamook Co., Nestucca River; species present: *D. coloradensis.*
3, Yamhill Co., Willamina Creek; species present: *D. coloradensis.*
4, Benton Co., Marys River; species present: *D. coloradensis.*
5, Benton Co., Rock Creek ; species present: *D. coloradensis.*
6, Benton Co., South Fork Alsea River; species present: *D. coloradensis.*
7, Benton Co., Crooked Creek; species present: *D. coloradensis.*
8, Lane Co., Wolf Creek; species present: *D. coloradensis.*
9, Lane Co., Wildcat Creek; species present: *D. coloradensis.*
10, Josephine Co., Grave Creek; species present: *D. personata, D. coloradensis.*
11, Douglas Co., Elk Creek; species present: *D. coloradensis.*
12, Douglas Co., South Umpqua River; species present: *D. coloradensis.*
13, Lane Co., South Fork McKenzie River; species present: *D. coloradensis.*
14, Lane Co., Roaring River; species present: *D. inyoensis.*
15, Clackamas Co., Clackamas River; species present: *D. coloradensis.*
16, Clackamas Co., Roaring River; species present: *D. inyoensis, D. coloradensis.*
17, Klickitat Co., Major Creek; species present: *D. vernalis.*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125°
124°
123°
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121°
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45°
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42°
WA
ID
Oregon
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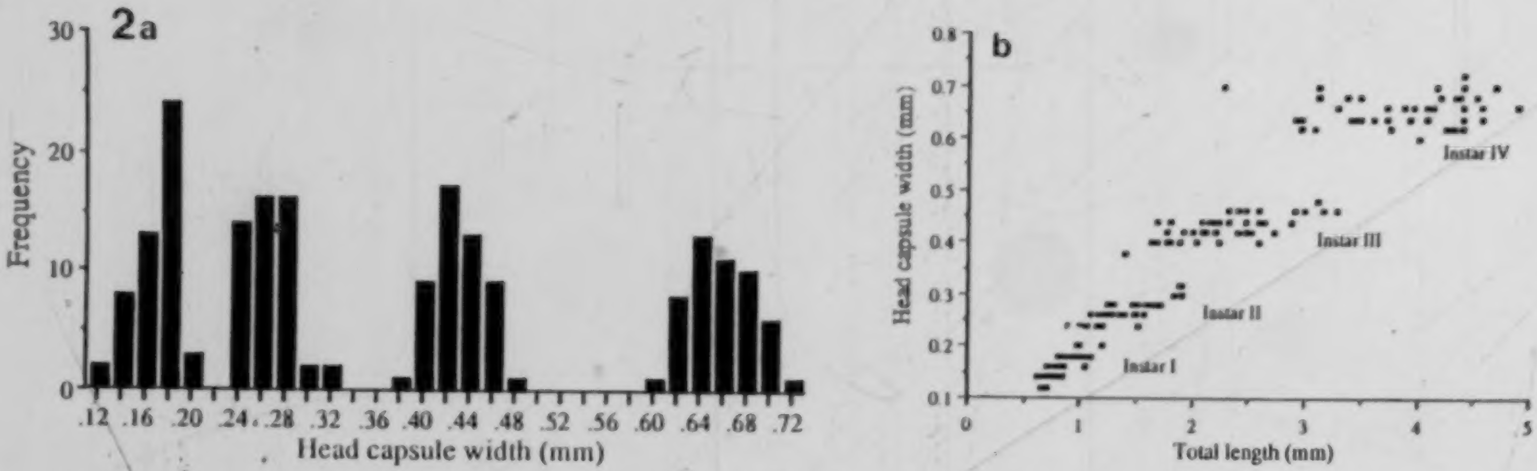
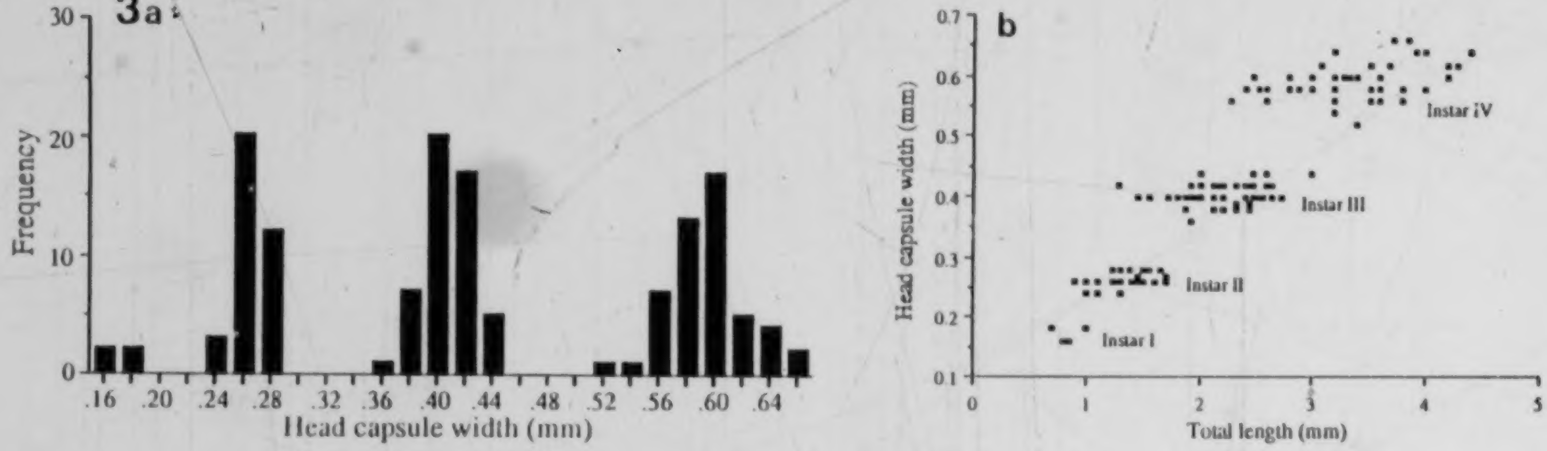
13
14
15
16
17
0 25 50 100 150
Kilometers

Figures 2-3. Instar data for *Deuterophlebia* larvae.

Figure 2. *Deuterophlebia inyoensis* larval instar data: (**a**) histogram of head capsule width; (**b**) scattergram of head capsule width *vs.* total length. Sample size: 50 individuals per instar; data based mostly on Roaring River (Lane Co.) specimens.

Figure 3. *Deuterophlebia shasta* larval instar data: (**a**) histogram of head capsule width; (**b**) scattergram of head capsule width *vs.* total length. Sample size: instar I (4), instar II (35), instars III (50), instar IV (50); data based mostly on Smith River specimens.

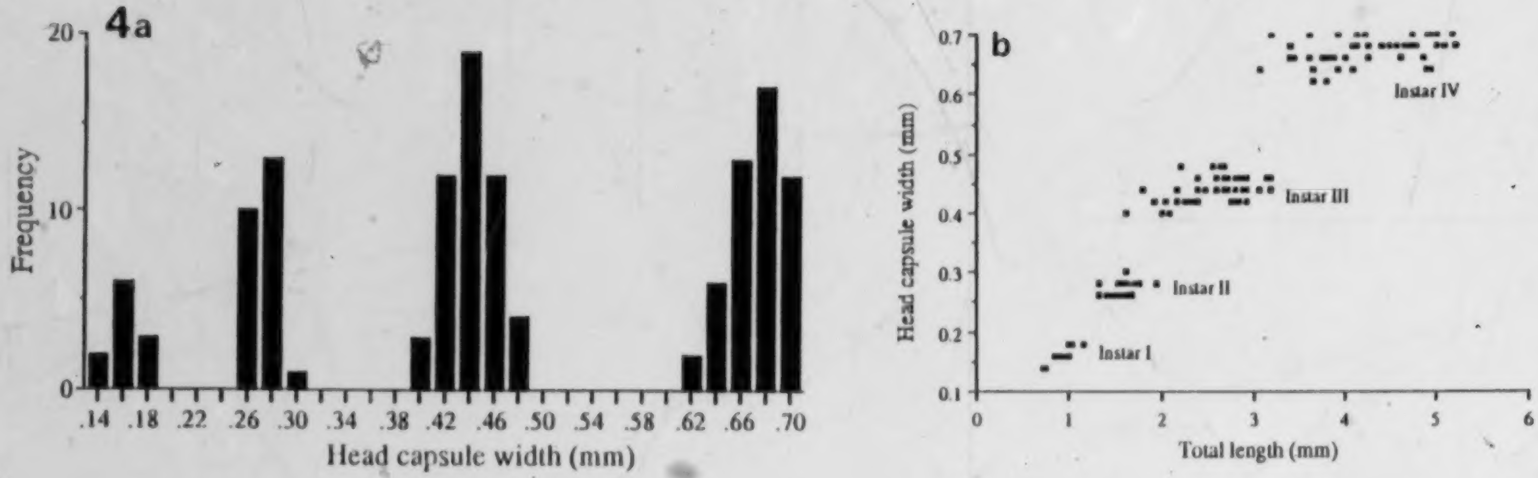

2a
Frequency
30
20
10
0
.12
.16
.20
.24
.28
.32
.36
.40
.44
.48
.52
.56
.60
.64
.68
.72
Head capsule width (mm)
b
Head capsule width (mm)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1
2
3
4
5
Total length (mm)
Instar I
Instar II
Instar III
Instar IV

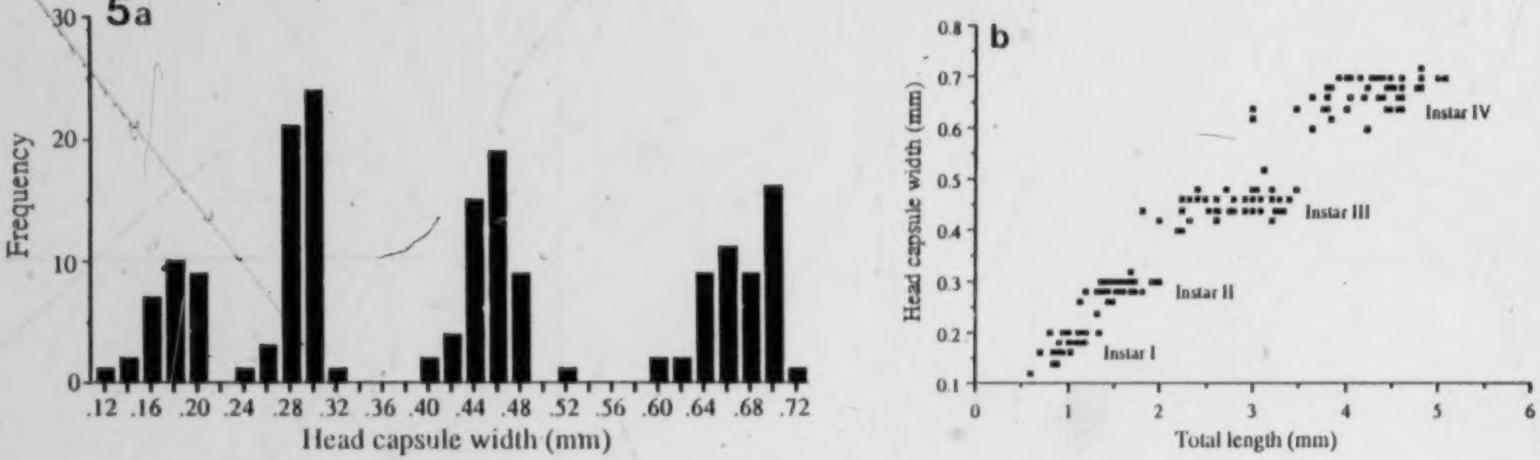

3a
Frequency
30
20
10
0
.16
.20
.24
.28
.32
.36
.40
.44
.48
.52
.56
.60
.64
Head capsule width (mm)
b
Head capsule width (mm)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1
2
3
4
5
Total length (mm)
Instar I
Instar II
Instar III
Instar IV

Figures 4-5. Instar data for *Deuterophlebia* larvae.

Figure 4. *Deuterophlebia personata* larval instar data: (**a**) histogram of head capsule width; (**b**) scattergram of head capsule width *vs*. total length. Sample size: instar I (18), instar II (27), instars III (50), instar IV (50); data based mostly on Cedar Creek specimens.

Figure 5. *Deuterophlebia vernalis* larval instar data: (**a**) histogram of head capsule width; (**b**) scattergram of head capsule width *vs*. total length. Sample size: instar I (29), instar II (50), instars III (50), instar IV (50); data based on Major Creek specimens.

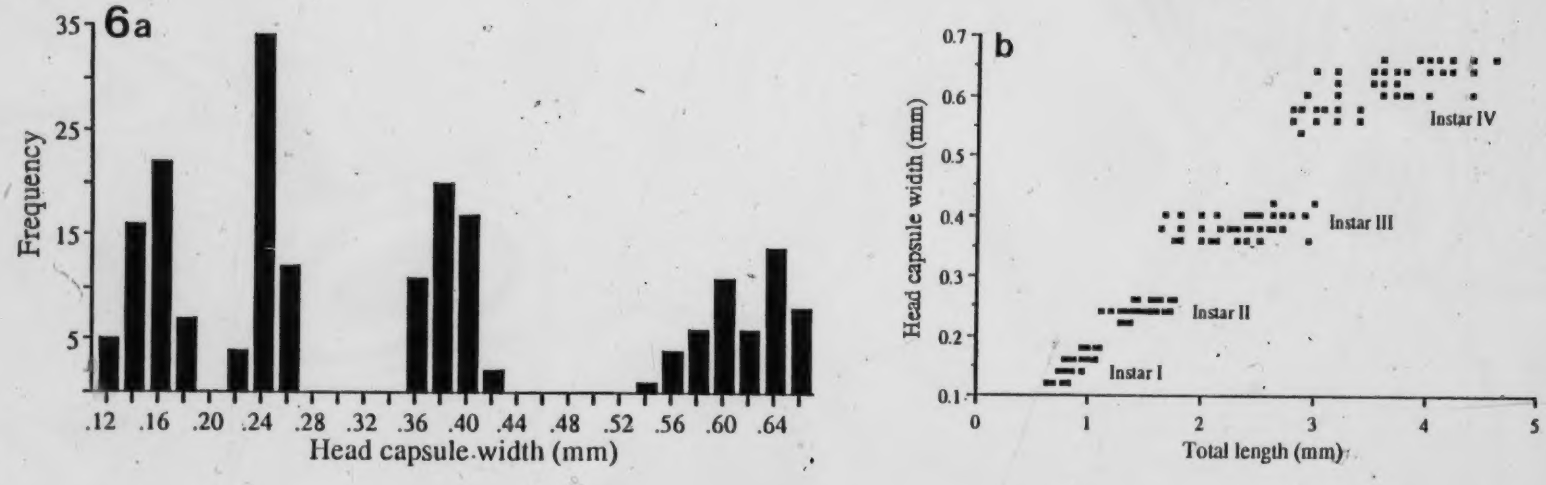

4a
Frequency
20
10
0
.14 .18 .22 .26 .30 .34 .38 .42 .46 .50 .54 .58 .62 .66 .70
Head capsule width (mm)
b
Head capsule width (mm)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Instar IV
Instar III
Instar II
Instar I
0 1 2 3 4 5 6
Total length (mm)


5a
Frequency
30
20
10
0
.12 .16 .20 .24 .28 .32 .36 .40 .44 .48 .52 .56 .60 .64 .68 .72
Head capsule width (mm)
b
Head capsule width (mm)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Instar IV
Instar III
Instar II
Instar I
0 1 2 3 4 5 6
Total length (mm)

Figures 6-7. Instar data for *Deuterophlebia* larvae.

Figure 6. *Deuterophlebia coloradensis* larval instar data: (**a**) histogram of head capsule width; (**b**) scattergram of head capsule width *vs*. total length. Sample size: 50 individuals per instar; data based on South Fork Alsea River specimens.

Figure 7. *Deuterophlebia coloradensis* larval instar data: (**a**) histogram of head capsule width; (**b**) scattergram of head capsule width *vs*. total length. Sample size: 50 individuals per instar; data based on Clackamas River specimens.


6a
35
25
15
5
Frequency
.12 .16 .20 .24 .28 .32 .36 .40 .44 .48 .52 .56 .60 .64
Head capsule width (mm)
b
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Head capsule width (mm)
Instar IV
Instar III
Instar II
Instar I
0 1 2 3 4 5
Total length (mm)

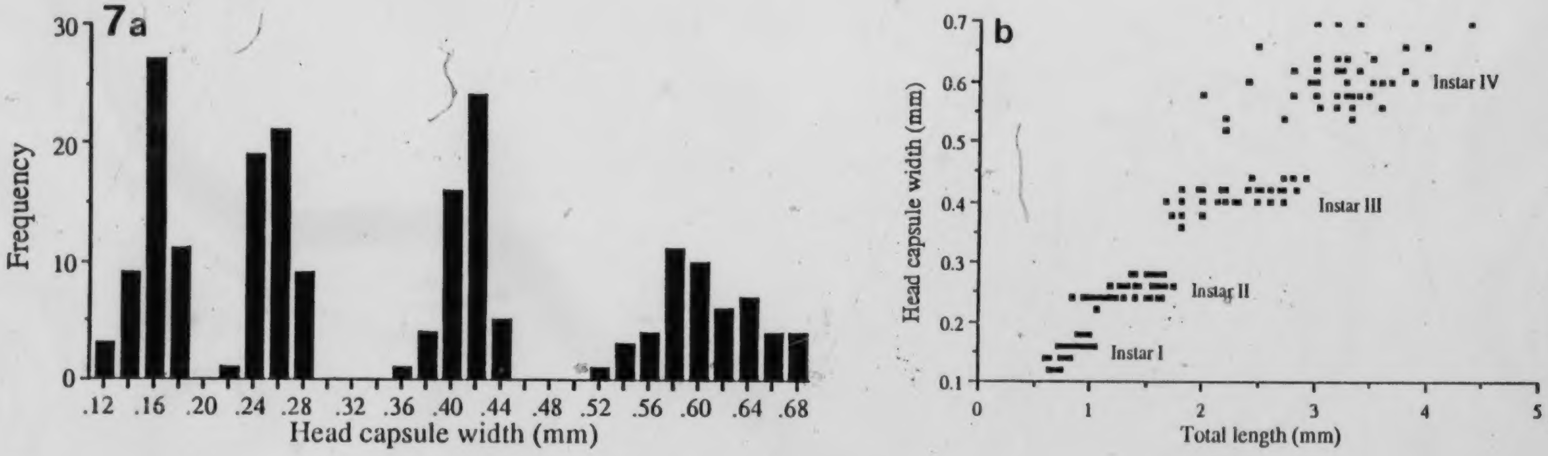
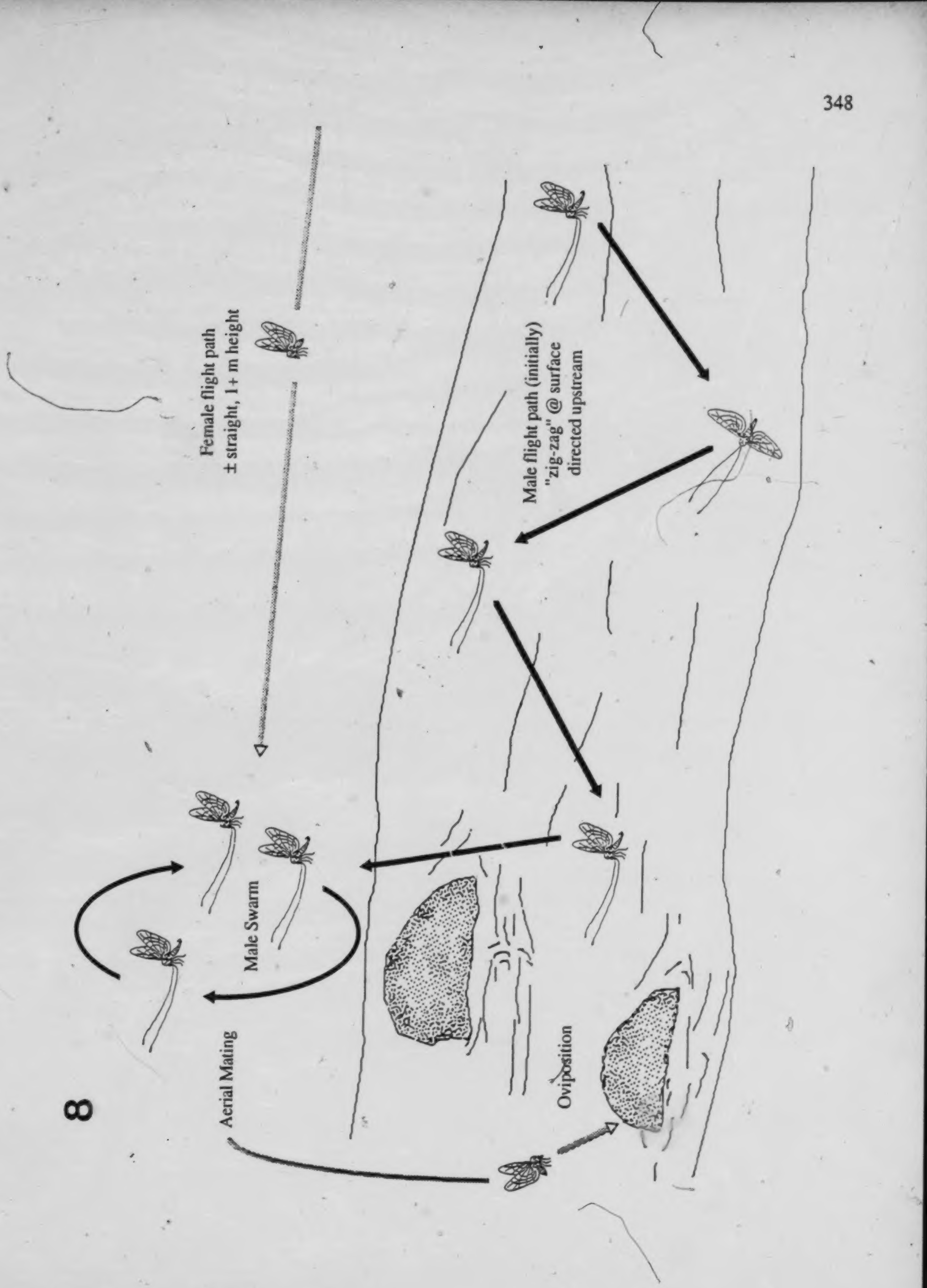

7a
30
20
10
0
Frequency
.12 .16 .20 .24 .28 .32 .36 .40 .44 .48 .52 .56 .60 .64 .68
Head capsule width (mm)
b
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Head capsule width (mm)
Instar IV
Instar III
Instar II
Instar I
0 1 2 3 4 5
Total length (mm)

Figure 8. Diagrammatic summary of flight behaviour of adult *Deuterophlebia*.



8

Female flight path
± straight, 1+ m height
Male flight path (initially)
"zig-zag" @ surface
directed upstream
Male Swarm
Aerial Mating
Oviposition

Figure 9. Relationship between estimated fecundity (# of eggs / female pupa) and total length of female pupa: (**a**) *D. inyoensis*; (**b**) *D. shasta*; (**c**) *D. personata*, (**d**) *D. vernalis*; (**e**) *D. coloradensis* (South Fork Alsea River).

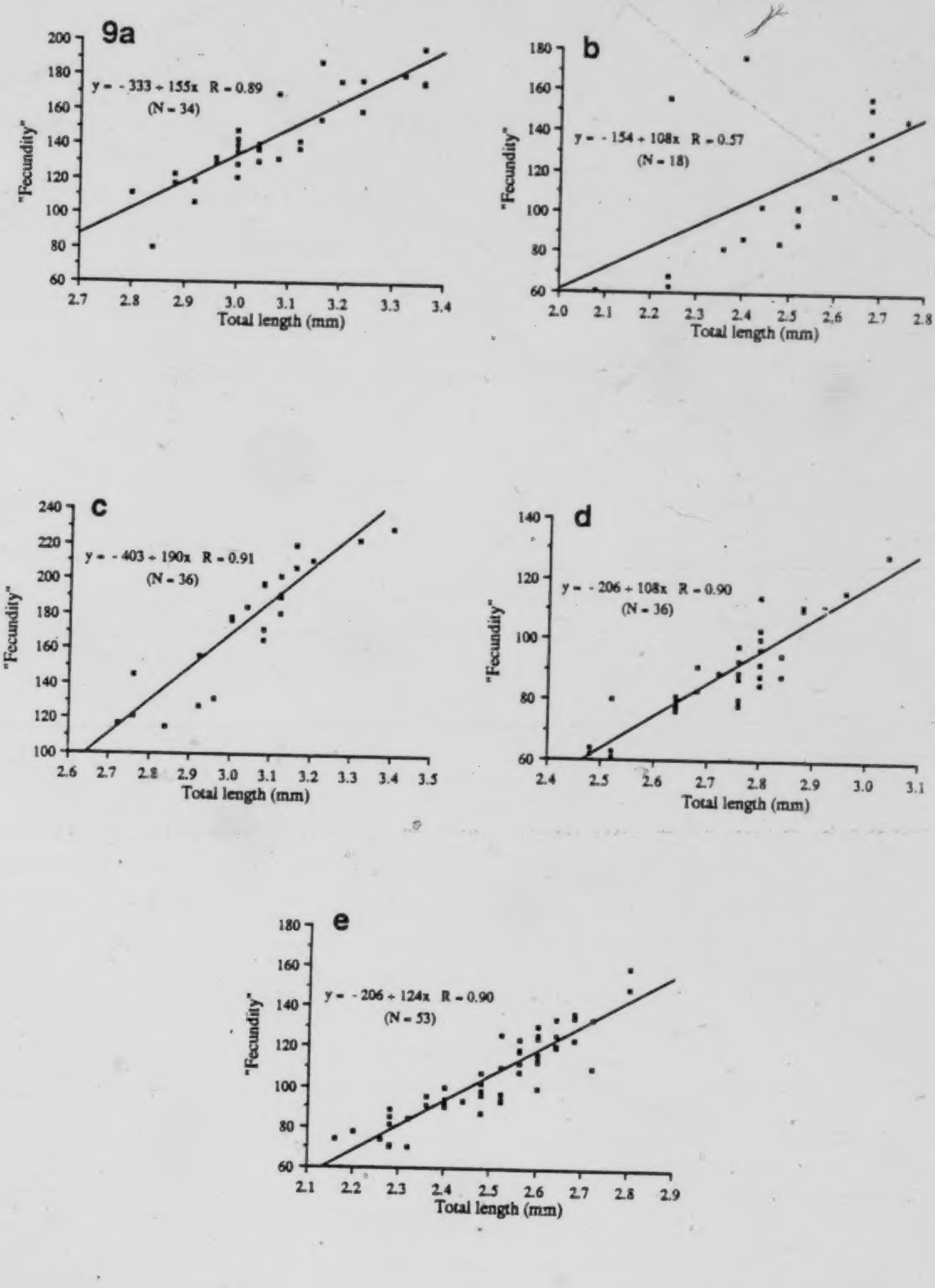

9a
y = - 333 + 155x R = 0.89
(N = 34)
"Fecundity"
Total length (mm)
60
80
100
120
140
160
180
200
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
b
y = - 154 + 108x R = 0.57
(N = 18)
"Fecundity"
Total length (mm)
60
80
100
120
140
160
180
2.0
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
c
y = - 403 + 190x R = 0.91
(N = 36)
"Fecundity"
Total length (mm)
100
120
140
160
180
200
220
240
2.6
2.7
2.8
2.9
3.0
3.1
3.2
3.3
3.4
3.5
d
y = - 206 + 108x R = 0.90
(N = 36)
"Fecundity"
Total length (mm)
60
80
100
120
140
2.4
2.5
2.6
2.7
2.8
2.9
3.0
3.1
e
y = - 206 + 124x R = 0.90
(N = 53)
"Fecundity"
Total length (mm)
60
80
100
120
140
160
180
2.1
2.2
2.3
2.4
2.5
2.6
2.7
2.8
2.9

Figure 10. Phenological data for Cedar Creek population of *D. personata*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 10a); numbers enclosed by brackets refer to sample sizes for each date.

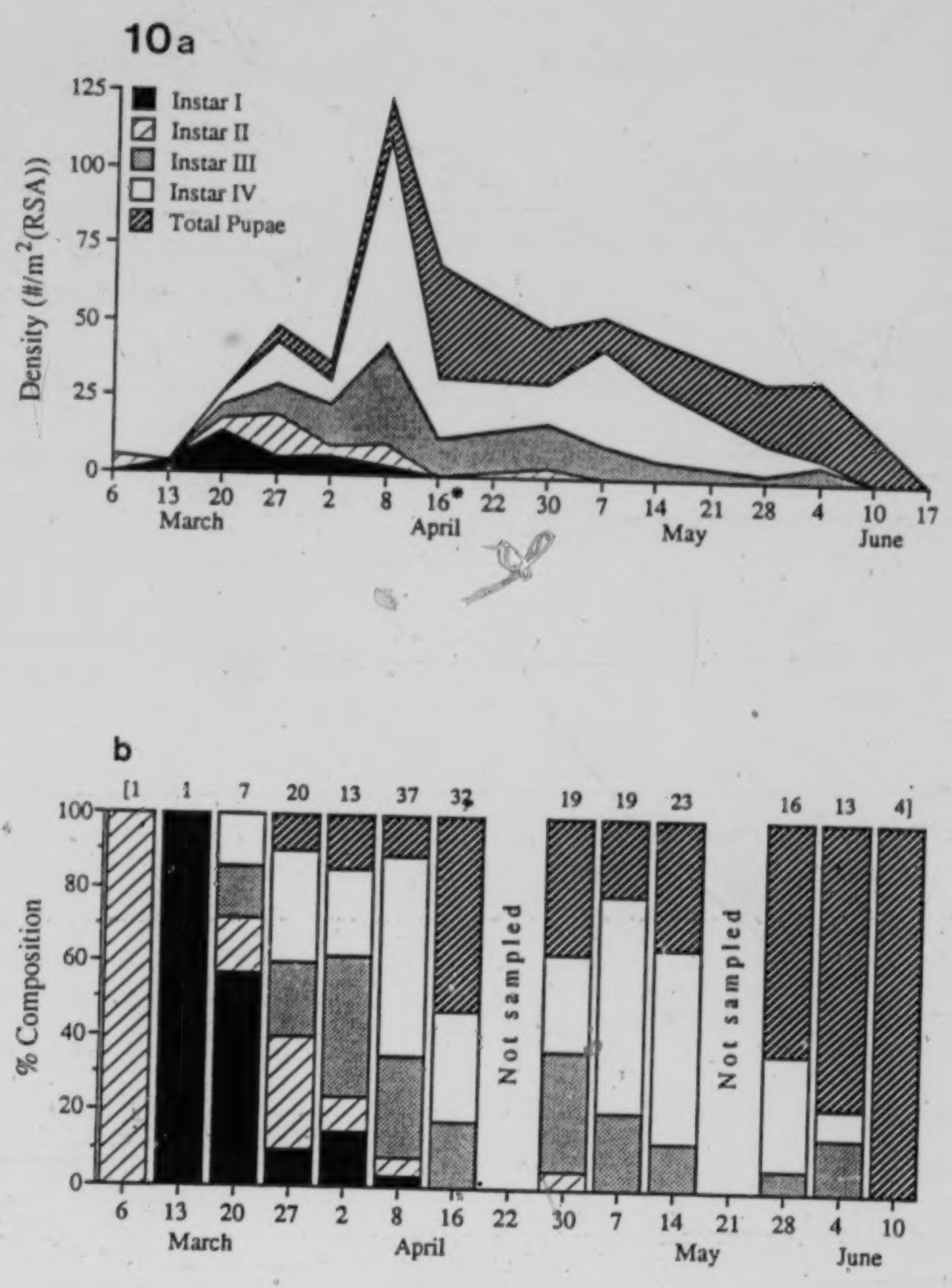
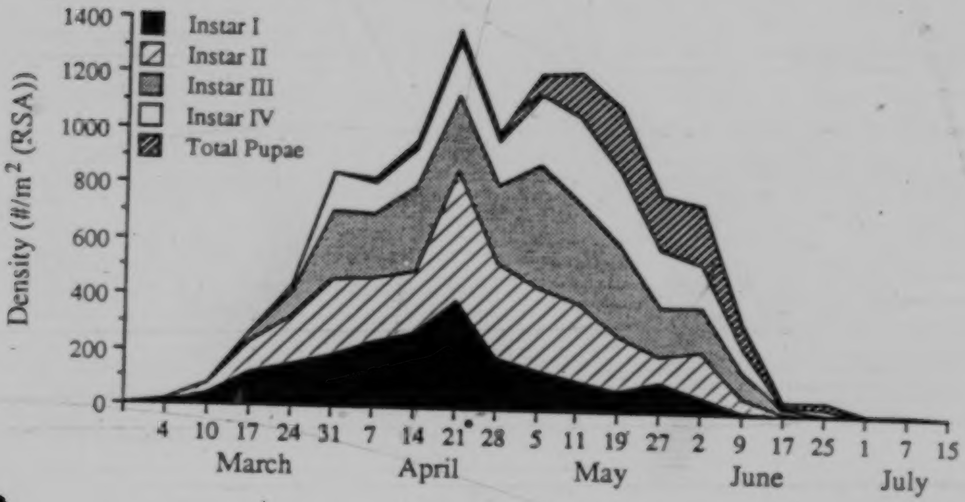

10a
Density (#/m²(RSA))
125
100
75
50
25
0
Instar I
Instar II
Instar III
Instar IV
Total Pupae
6
13
20
27
2
8
16*
22
30
7
14
21
28
4
10
17
March
April
May
June
b
[1
1
7
20
13
37
32
19
19
23
16
13
4]
% Composition
100
80
60
40
20
0
Not sampled
Not sampled
6
13
20
27
2
8
16
22
30
7
14
21
28
4
10
March
April
May
June

Figure 11. Phenological data for South Fork Alsea River population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 11a); numbers enclosed by brackets refer to sample sizes for each date.

11a


Instar I
Instar II
Instar III
Instar IV
Total Pupae
Density (#/m² (RSA))
1400
1200
1000
800
600
400
200
0
4
10
17
24
31
7
14
21
28
5
11
19
27
2
9
17
25
1
7
15
March
April
May
June
July

b

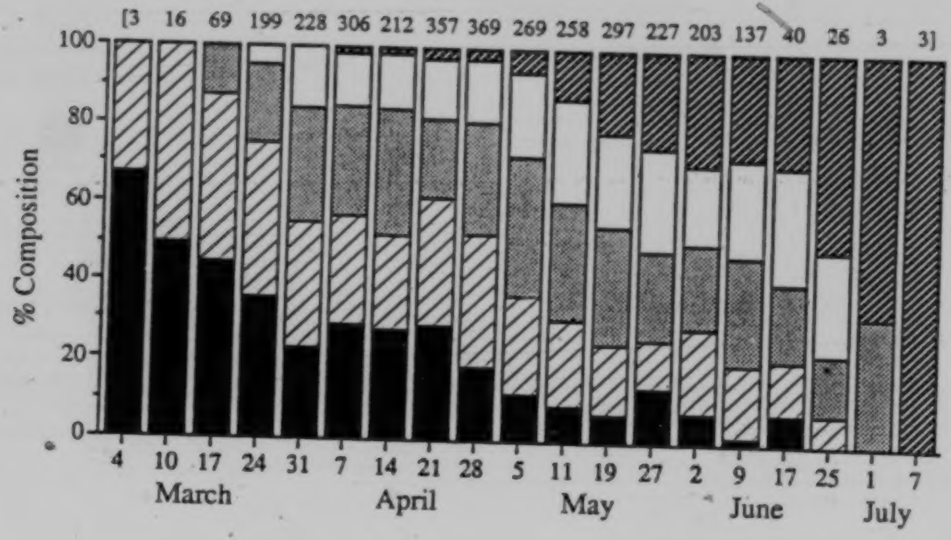
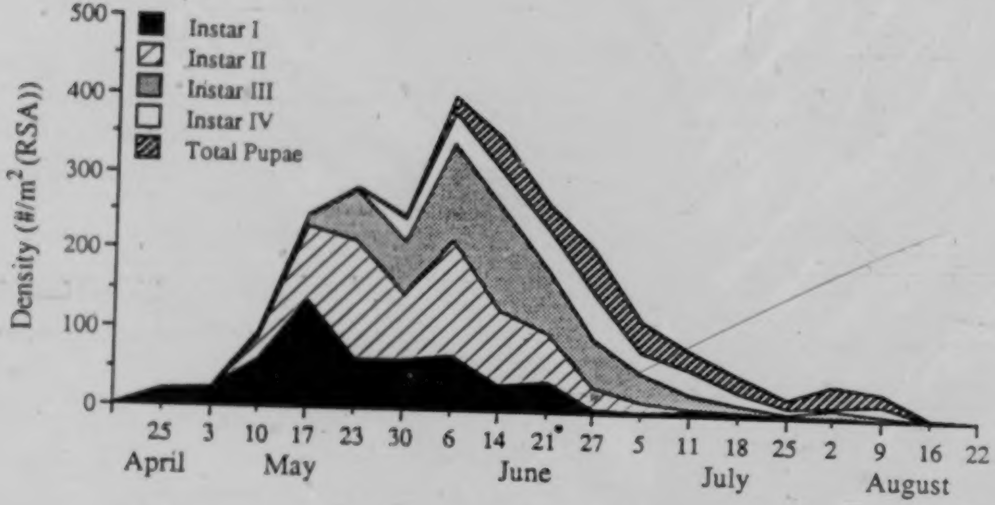

[3 16 69 199 228 306 212 357 369 269 258 297 227 203 137 40 26 3 3]
% Composition
100
80
60
40
20
0
4
10
17
24
31
7
14
21
28
5
11
19
27
2
9
17
25
1
7
March
April
May
June
July

Figure 12. Phenological data for South Fork McKenzie River population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 12a); numbers enclosed by brackets refer to sample sizes for each date.

12a


Instar I
Instar II
Instar III
Instar IV
Total Pupae
Density (#/m^2 (RSA))
500
400
300
200
100
0
25
3
10
17
23
30
6
14
21
27
5
11
18
25
2
9
16
22
April
May
June
July
August

b

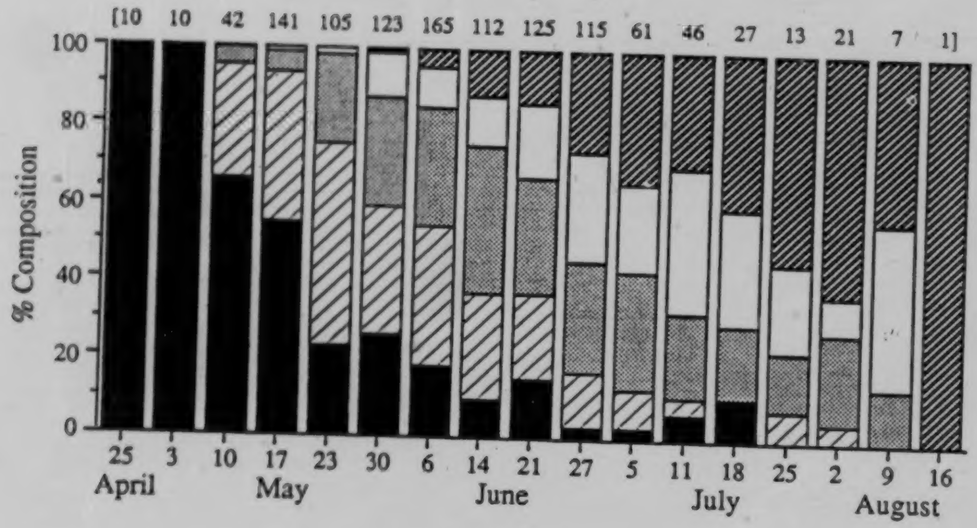

[10
10
42
141
105
123
165
112
125
115
61
46
27
13
21
7
1]
% Composition
100
80
60
40
20
0
25
3
10
17
23
30
6
14
21
27
5
11
18
25
2
9
16
April
May
June
July
August

Figure 13. Phenological data for Roaring River (Lane Co.) population of *D. inyoensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 13a); numbers enclosed by brackets refer to sample sizes for each date.

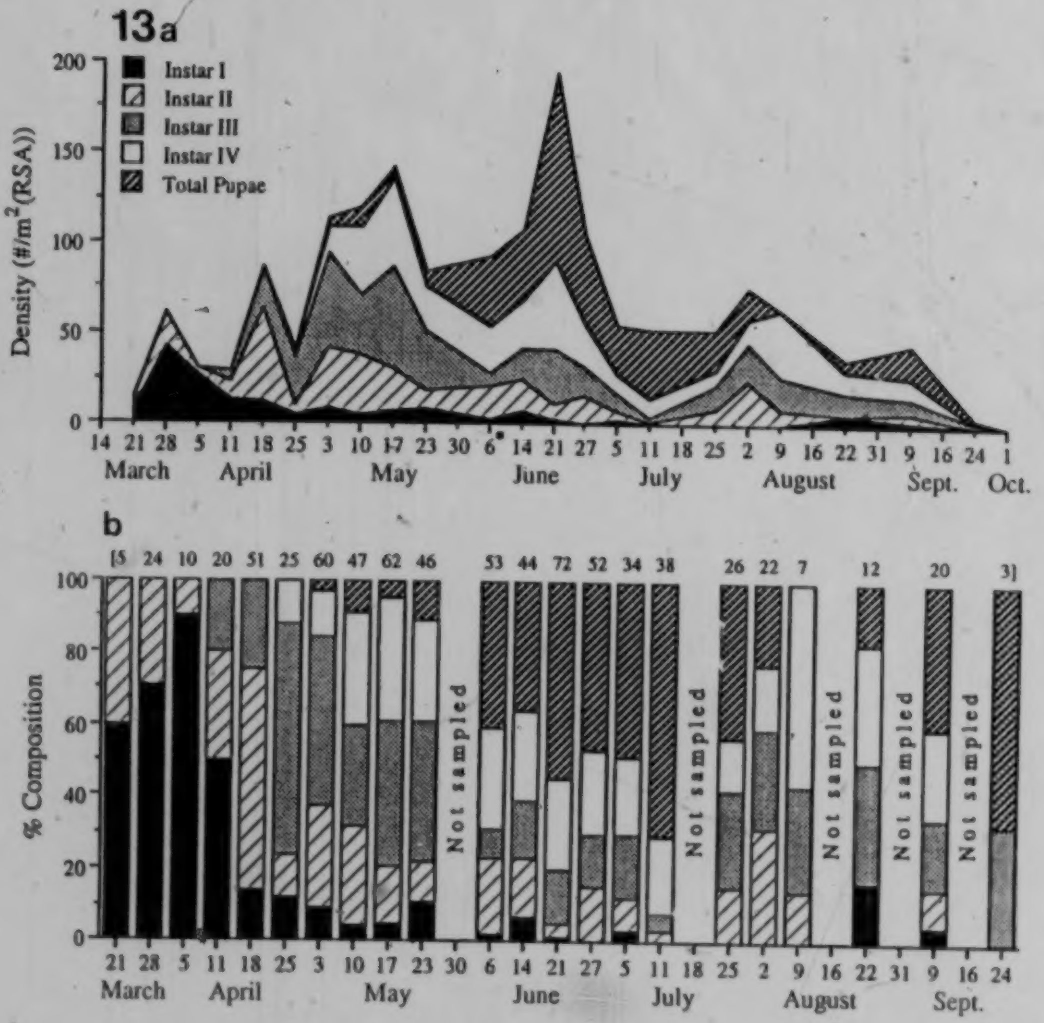

13a
Instar I
Instar II
Instar III
Instar IV
Total Pupae
Density (#/m^2(RSA))
200
150
100
50
0
14 21 28 5 11 18 25 3 10 17 23 30 6* 14 21 27 5 11 18 25 2 9 16 22 31 9 16 24 1
March April May June July August Sept. Oct.
b
15 24 10 20 51 25 60 47 62 46 53 44 72 52 34 38 26 22 7 12 20 31
% Composition
100
80
60
40
20
0
Not sampled
Not sampled
Not sampled
Not sampled
Not sampled
21 28 5 11 18 25 3 10 17 23 30 6 14 21 27 5 11 18 25 2 9 16 22 31 9 16 24
March April May June July August Sept.

Figure 14. Phenological data for Clackamas River population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 14a); numbers enclosed by brackets refer to sample sizes for each date.

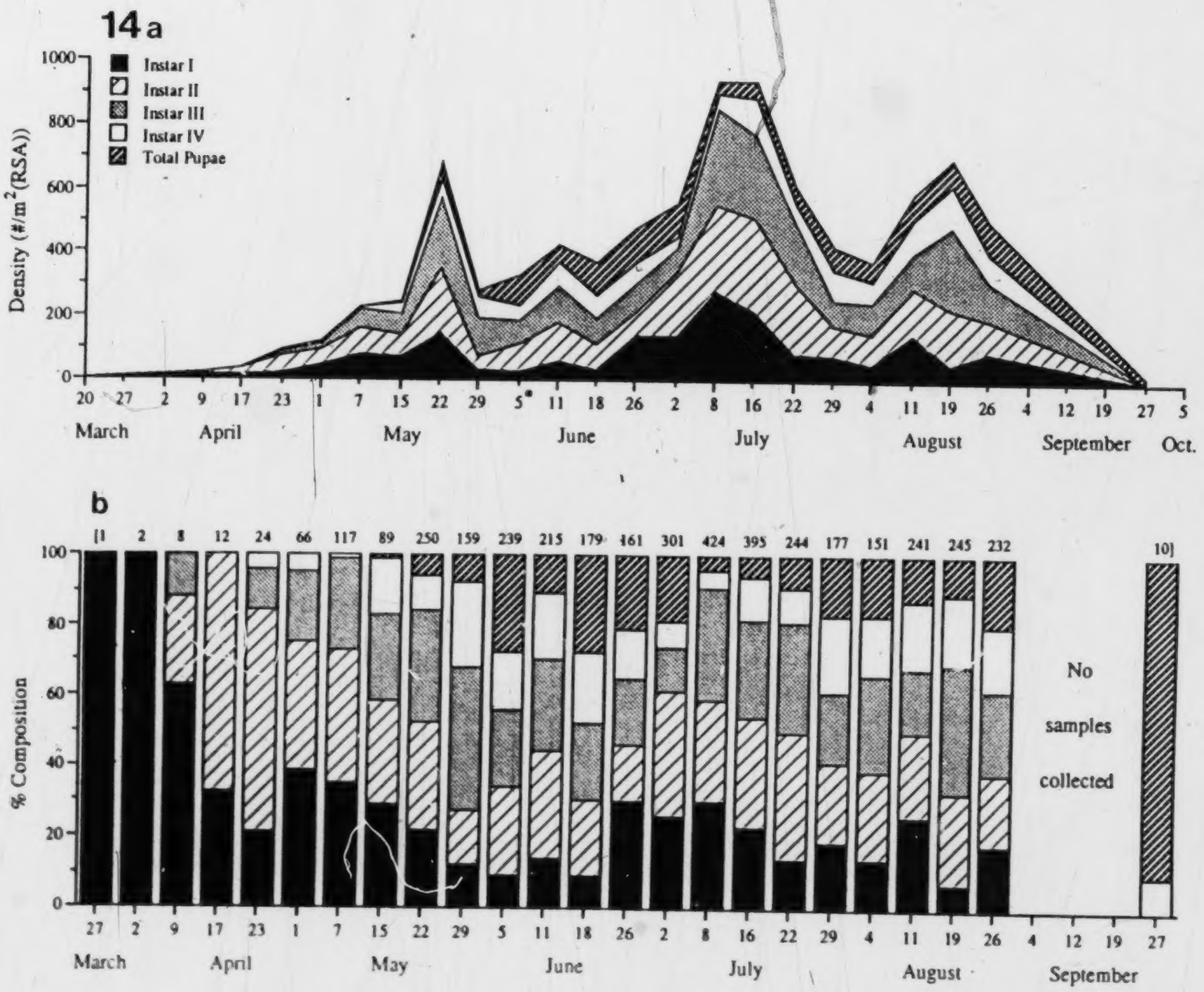
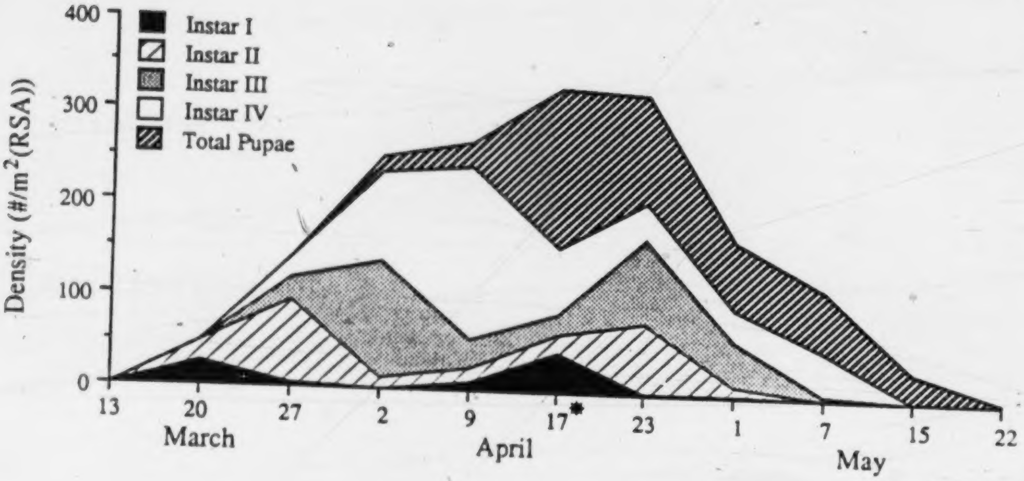

14 a
Density (#/m^2(RSA))
1000
800
600
400
200
0
Instar I
Instar II
Instar III
Instar IV
Total Pupae
20 27 2 9 17 23 1 7 15 22 29 5* 11 18 26 2 8 16 22 29 4 11 19 26 4 12 19 27 5
March April May June July August September Oct.
b
% Composition
100
80
60
40
20
0
[1 2 8 12 24 66 117 89 250 159 239 215 179 161 301 424 395 244 177 151 241 245 232 10]
No samples collected
27 2 9 17 23 1 7 15 22 29 5 11 18 26 2 8 16 22 29 4 11 19 26 4 12 19 27
March April May June July August September

Figure 15. Phenological data for Major Creek population of *D. vernalis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 15a); numbers enclosed by brackets refer to sample sizes for each date.

15a


400
300
200
100
0
Density (#/m²(RSA))
Instar I
Instar II
Instar III
Instar IV
Total Pupae
13
20
27
2
9
17*
23
1
7
15
22
March
April
May

b

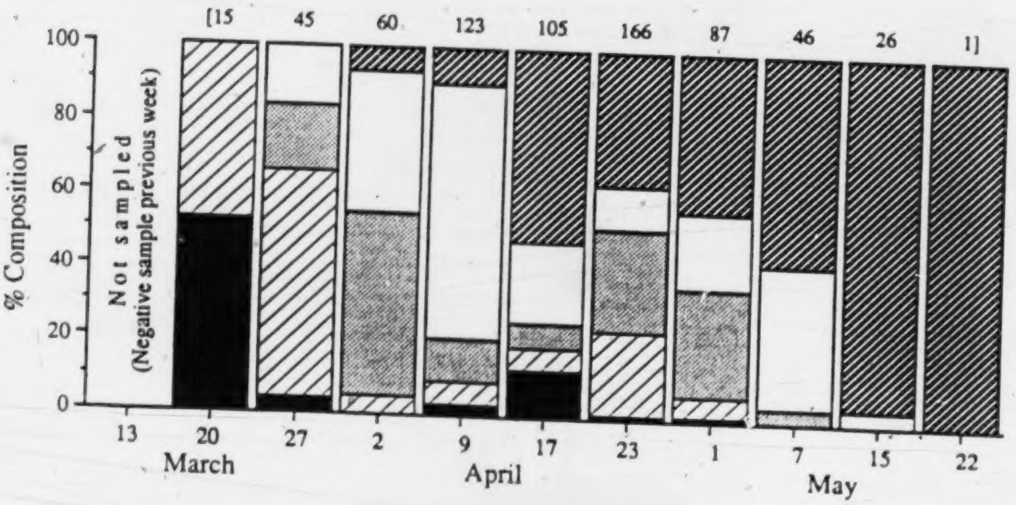

[15
45
60
123
105
166
87
46
26
1]
100
80
60
40
20
0
% Composition
Not sampled
(Negative sample previous week)
13
20
27
2
9
17
23
1
7
15
22
March
April
May

Figure 16. Generalized pattern of longitudinal and temporal distribution of *D. inyoensis* and *D. coloradensis* in a Cascade Range stream.

16

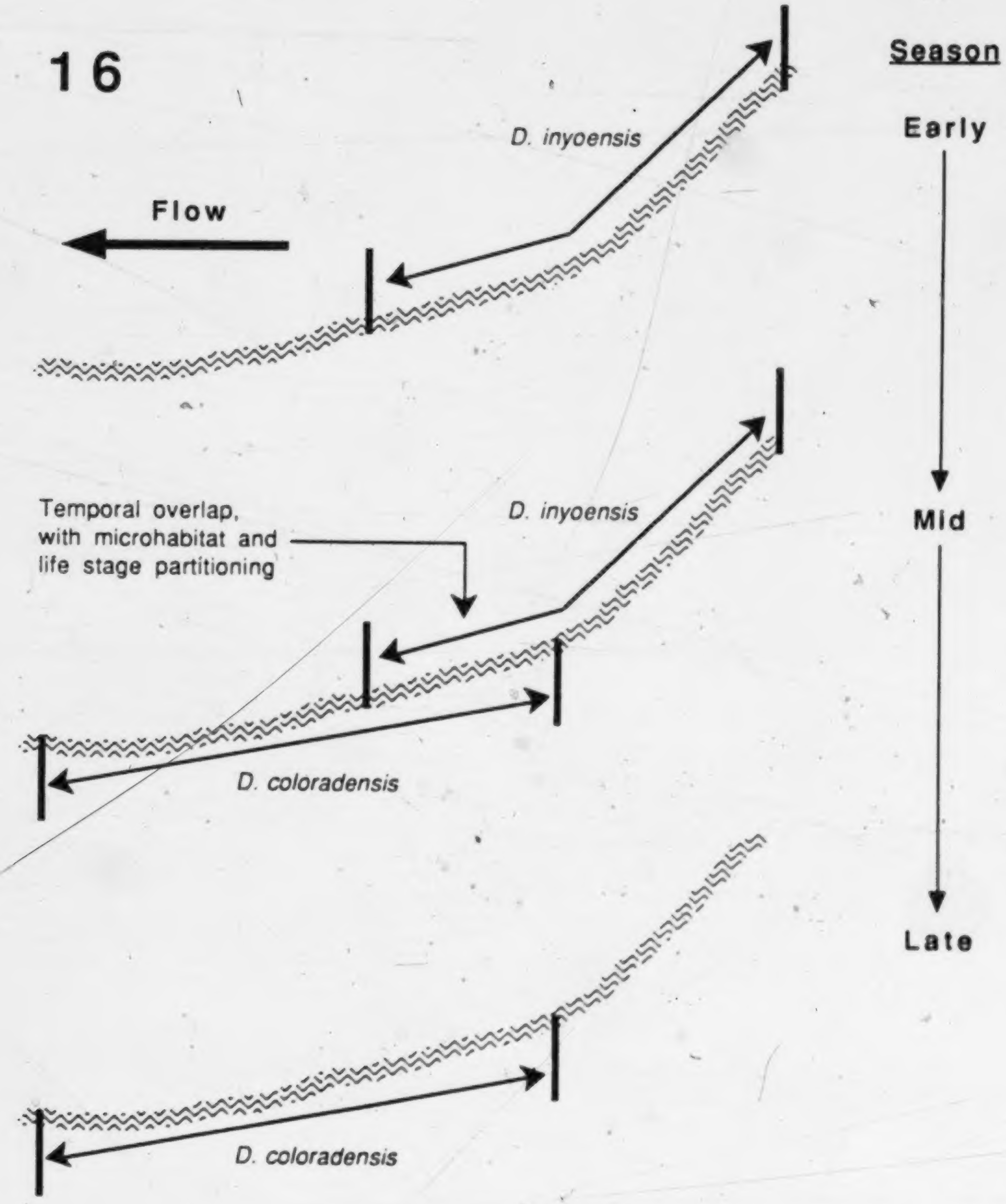
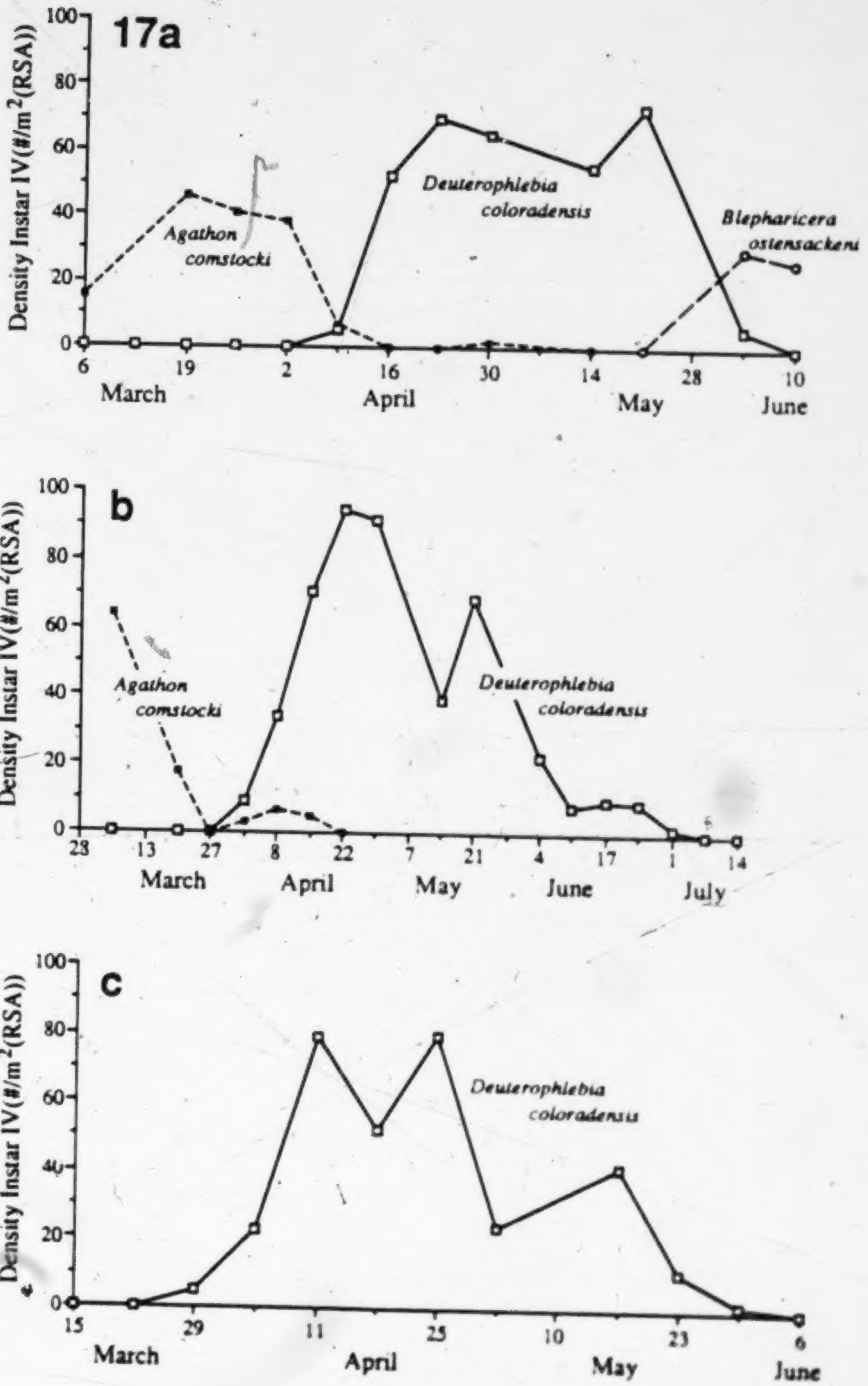

Season
Early
Mid
Late
Flow
D. inyoensis
D. inyoensis
Temporal overlap, with microhabitat and life stage partitioning
D. coloradensis
D. coloradensis

Figure 17. Larval instar IV density (number per square meter (rock surface area)) of sympatric species of Deuterophlebiidae (*D. coloradensis*) and Blephariceridae from Coast Range streams: (**a**) 1986 data for Willamina Creek (site 3); (**b**) 1986 data for Nestucca River (site 2); (**c**) 1986 data for Wolf Creek (site 8).


17a
Density Instar IV(#/m²(RSA))
100
80
60
40
20
0
Agathon comstocki
Deuterophlebia coloradensis
Blepharicera ostensackeni
6
19
2
16
30
14
28
10
March
April
May
June
b
Density Instar IV(#/m²(RSA))
100
80
60
40
20
0
Agathon comstocki
Deuterophlebia coloradensis
28
13
27
8
22
7
21
4
17
1
14
March
April
May
June
July
c
Density Instar IV(#/m²(RSA))
100
80
60
40
20
0
Deuterophlebia coloradensis
15
29
11
25
10
23
6
March
April
May
June

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6. PHYLOGENETIC AND ZOOGEOGRAPHIC RELATIONSHIPS OF THE WORLD SPECIES OF MOUNTAIN MIDGES (DIPTERA: DEUTEROPHLEBIIDAE).

6.1 Synopsis

A cladistic analysis of larval, pupal, and adult characters provides a framework for discussion about the phylogeny and zoogeography of world species of Deuterophlebiidae. Based on features of the adult male, *D. brachyrhina* Courtney is considered the sister taxon of all other deuterophlebiids. Within the latter clade, *D. oporina* Courtney is proposed as the sister taxon of the remaining species, which, in turn, has *D. inyoensis* Kennedy as the most plesiotypic species. Relationships between derivative members of the family are based primarily on larval and pupal characters; however, lack of information about the immature stages of Palaearctic species necessitates consideration of other reconstructions. A preliminary zoogeographic analysis of the Deuterophlebiidae suggests that the contemporary Nearctic fauna originated from at least two invasions of North America.

6.2 Introduction

The nematocerous family Deuterophlebiidae is one of the most specialized and distinctive of dipterous insects. The immature stages are aquatic, typically inhabiting torrential mountain streams. Adults are non-feeding, and live for only a few hours. The Deuterophlebiidae contains 14 species, eight from eastern and central Asia (Edwards 1922, Kitakami 1938; Jedlicka and Halgos 1981, Courtney *in prep*[1]) and six from western North America (Pennak 1945; Wirth 1951; Kennedy 1958, 1960, Courtney *in press 2*[1]).

Previous systematic research on the Deuterophlebiidae has dealt either with familial relationships (*e.g.*, Hennig 1973; Rohdendorf 1974, Wood and Borkent *in press*, Courtney

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[1] See also chapter 4

in press 1[1]), or accounts of new species (*e.g.*, Kitakami 1938; Pennak 1945; Wirth 1951; Kennedy 1958). No one has bridged the gap between these rather different levels of systematic research. This study will attempt to construct this bridge, by investigating the phylogenetic relationships of constituent species of the Deuterophlebiidae. Larval, pupal and adult characters of mountain midges are evaluated by cladistic methods (*sensu* Hennig 1966). This analysis provides a basis for discussion about zoogeography of world species of Deuterophlebiidae.

6.3 Materials and Methods

6.3.1 Materials. Larvae, pupae and adults of all Nearctic and most Palaearctic species of *Deuterophlebia* were examined. This study was based primarily on material from collections of the author and various museums (see chapters 2 and 4 for complete listings).

6.3.2. Specimen Preparation. Specimens were prepared as outlined in Courtney (*in press 1*) and Courtney (*in press 2*). Material was examined using a variety of techniques (*e.g.*, whole-animal slide mounts, dissections, sections, scanning electron microscope (SEM)).

6.3.3. Terms for Structures. For most taxa, structural terms follow the *Manual of Nearctic Diptera* (*i.e.*, Teskey (1981) for larvae, McAlpine (1981) for adults). Deviations from this system, or new terms specifically applicable to the Deuterophlebiidae, are based on Courtney (*in press 1*) and Courtney (*in press 2*).

6.3.4 Phylogenetic Methods. Phylogenetic relationships of the world species of *Deuterophlebia* Edwards were determined using cladistic methods (*sensu* Hennig 1966), as outlined earlier (chapter 3). Evidence supporting a sister group relationship between the Deuterophlebiidae and Blephariceridae was provided elsewhere (chapters 2 and 3), and polarity decisions for ingroup phylogenetic analyses are based on the assumption that blepharicerids are the immediate outgroup of deuterophlebiids.

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[1] See also chapters 2 and 3.

Phylogenetic interpretation of many morphological characters can depend on an understanding of the ecology of a group (*e.g.*, see discussion of capitate leg macrotrichia). In the present study, ecological data are based primarily on observations of Nearctic species, and comparable ecologies for Palaearctic species are assumed

Cladograms were drawn with the aid of software programs available for Macintosh™ microcomputers. Alternate reconstructed phylogenies were compared through both a character-by-character analysis and with MacClade™ (version 2.1 - Maddison and Maddison 1987), a Macintosh™ program based on character compatibility and parsimony.

6.4 Character Analysis

Character numbers used in the discussion correspond to those in the character matrix (Table 1) and cladograms (Fig. 1, 2). For each character, alternate (*i.e.*, hypothesized plesiotypic and apotypic) character states are listed. Because of time constraints involved in preparation of this thesis, I present a somewhat abbreviated version of the character analysis. Several characters that were included in the MacClade analysis have been deleted from the present discussion, either because they represent autapotypies, or because they show extreme homoplasy, even within a single taxon. With few exceptions (characters 8, 10, 11?), the following discussion is restricted to characters which provide the most compelling evidence of relationships. Because of uncertainty about the relationships of derivative members of the family, alternate reconstructions are given.

The distribution of character states in the Deuterophlebiidae (and their outgroup, the Blephariceridae) is summarized in a character matrix (Table 1). Symbols used in the matrix are as follows[1]: "0" refers to the plesiotypic state; "1" refers to the apotypic state, or the first stage of a hypothesized transformation sequence; "2" refers to the subsequent stage of any transformation sequence; the presence of multiple character states within a particular taxon is indicated by numbers separated by a slash mark (*e.g.*, "0/1").

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[1] The same notation is used in the discussion of characters, if a transformation sequence is involved.

6.4.1 Larva

Character 1. *sensilla* prl *simple, setiform (plesiotypic) / sensilla* prl *branched, with two or three filaments (apotypic).*

Blephariceríd larvae demonstrate a variety of sensillar structures (Hogue 1987), but only rarely are these branched. Thus, the presence of simple sensilla is considered a groundplan feature of the Deuterophlebiidae. Among species for which larvae are known, the plesiotypic state occurs only in *D. inyoensis* Kennedy (see Fig. 4.3), *D. shasta* Wirth and possibly *D. nipponica* Kitakami[1]. This arrangement is also evident in *D.* sp. B (*sensu* chapter 4). The apotypic state (see Fig. 4.2) helps define two species groups, hereafter called the "*tyosenensis* group" (= *D. tyosenensis* Kitakami, *D. bicarinata* Courtney, *D. sajanica* Jedlicka and Halgos, *D. shasta* and *D. personata* Courtney) and "*coloradensis* group" (= *D.vernalis* Courtney, *D. nielsoni* Kennedy and *D. coloradensis* Pennak). Due to lack of material for examination, this character state has not been determined definitively for *D. tyosenensis*; it is assumed that this species demonstrates the same condition as other members of the clade. I interpret the condition in *D. shasta* as a reversal.

Character 2. *sensilla* at *and* mt *simple, setiform (plesiotypic) / sensilla* at *and* mt *branched into two or three setiform filaments (apotypic).*

The distribution of character states (*cf.* Figs. 4.4a, 4.4b) is identical to that of character 1.

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[1] The description given by Kitakami (1938) suggests that all thoracic sensilla are simple; however, this interpretation is admittedly tenuous. Only one, badly damaged specimen was available for examination, and chaetotaxic characters could not be evaluated.

Character 3. *clypeal lobe uniformly dark or with distinct pattern (plesiotypic) / clypeal lobe uniformly pale (apotypic).*

Color patterns are relatively homoplastic in some deuterophlebiids (*e.g.*, *D. coloradensis*, see chapter 4); however, color of the clypeal lobe is a rather consistent feature. The clypeal lobe is uniformly pale in only two species, *D. nielsoni* and *D. coloradensis*. *Deuterophlebia bicarinata* exhibits a similar, but presumably non-homologous arrangement, with the basal part of the clypeal lobe darkly pigmented and the apical part pale. The presence of a pale clypeal lobe supports monophyly of *D. nielsoni* and *D. coloradensis*.

Character 4. *sensilla group* ap *with two clusters of several digitiform sensilla (plesiotypic) / sensilla group* ap *with only two individual digitiform sensilla (apotypic).*

The plesiotypic state occurs in *D. inyoensis*, *D. bicarinata*, *D. sajanica*, and *D.* sp. B (see chapter 4, Fig. 4.4). The arrangement in *D. nipponica* and *D. tyosenensis* is unknown. Accepting phylogeny I (Fig. 1) requires that the apotypic state evolved independently in both *D. shasta* + *D. personata*, and the *D. coloradensis* group. Phylogeny II (Fig. 2) emphasizes larval chaetotaxy, using the apotypic state to define *D. shasta* + *D. personata* + *D. coloradensis* group, but at the expense of a second tritomy. Because of lack of information about chaetotaxy of Palaearctic species, I consider the latter hypothesis rather tenuous. Homologous structures could not be identified in the Blephariceridae.

Character 5. *instar II proleg with three rows of eversible crochets (plesiotypic) / instar II proleg with four rows of eversible crochets (apotypic).*

The number of crochet rows on the instar II proleg may be an extremely informative character. The deuterophlebiid proleg is one of the aberrant features of the family, and is markedly different from the proleg of larval Blephariceridae. Except for instar I, the deuterophlebiid proleg bears multiple rows of crochets. An increasing number of crochet rows presumably reflects greater structural specialization; therefore, the presence of three crochet rows in larval instar II is considered more plesiotypic than is four rows. This polarity decision supports either of the proposed phylogenies, since three crochet rows are present in *D. inyoensis* and *D. nipponica* (Kitakami 1938), and four are typical of the more apotypic Nearctic species. Unfortunately, instar II larvae are unknown in most Palaearctic species. Knowledge about the distribution of this character in Palaearctic species will provide a test for these hypotheses, as well as valuable insights on the relationships among the *tyosenensis* and *coloradensis* species groups.

6.4.2 Pupa

Character 6. *anterolateral margin of mesonotum without spines (plesiotypic) / anterolateral margin of mesonotum with anterolaterally projected spines above gill (apotypic).*

The plesiotypic state occurs in *D. inyoensis, D. nipponica, D.* sp. A (*sensu* chapter 4) and the "*coloradensis*" group (*e.g.*, Figs. 4.15, 4.21). In phylogeny I, the presence of mesonotal spines defines the *tyosenensis* species group. This character state is also found in *D.* sp. C (*sensu* chapter 4), a species presently known only from the pupal stage. Demonstration that this pupal morphotype is conspecific with a species known only from adults (*e.g.*, *D. blepharis* Courtney, *D. mirabilis* Edwards) would indicate that the presence of mesonotal spines is homoplastic. Homoplasy of this character is also suggested by the occurrence of pupae with short, curved mesonotal spines (Fig. 4.19) in certain *D. coloradensis* populations. The latter suggests that phylogeny II may be the more acceptable hypothesis; however, for reasons given above (*re.* character 4), I favour phylogeny I.

Character 7. *gill in the form of three, elongate, lateral filaments (plesiotypic) / gill in the form of three elongate, lateral filaments and one stout, posteriorly projected filament (apotypic).*

The plesiotypic state (*cf.* Figs. 4.28-4.30) occurs in most species in which pupae are known. The presence of four gill filaments (*cf.* Fig.4.27) is unique to *D. tyosenensis*, *D. bicarinata*, *D. sajanica*, and *D.* sp. C (*sensu* chapter 4). The apotypic state is considered the intermediate stage of a transformation series (see below).

Character 7a. *gill with posterior filament length subequal to width (plesiotypic) / gill with posterior filament relatively elongate, ca. twice as long as broad (apotypic).*

The apotypic state is the ultimate stage of the above transformation series, and is characteristic of only *D. bicarinata* and *D. sajanica.*

Character 8. *abdominal tergites bearing microtubercles (plesiotypic) / abdominal tergites without microtubercles (apotypic).*

The pupae of most species of mountain midge demonstrate the plesiotypic condition (*cf.* Figs. 4.41-4.46). Among species for which pupae are known, abdominal microtubercles are lacking from *D. tyosenensis*[1] and *D. shasta*. Pupal microsculpture is extremely useful for species identification (see chapter 4); however, the character is only tentatively used in phylogenetic analyses. Microsculptural arrangements may reflect environment rather than phylogenetic relationships and, even if the latter is assumed, establishing polarities is difficult. Because of marked microsculptural variability (*personal observation*) and an incomplete knowledge of relationships within the Blephariceridae, data for the outgroup provide few insights. For the present, I consider lack of microtubercles in *D. tyosenensis* and *D. shasta* as convergent.

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[1] Based on examination of a single specimen.

Character 9. *abdominal tergites bearing clusters of microtrichia, usually associated with microtubercles (plesiotypic) / abdominal tergites with microtrichia randomly distributed over cuticle, not distinctly associated with microtubercles (apotypic).*

The plesiotypic condition is typical of most deuterophlebiids (see Figs. 4.41-4.45). Among species with associated pupae, the apotypic state occurs only in *D. sajanica* and *D. bicarinata* (Fig. 4.46). However, microsculptural features of most Palaearctic species have not been definitively determined.

Character 10. *segmental boundaries between abdominal tergites simple, without perpendicular, secondary ridges (plesiotypic) / segmental boundaries between abdominal tergites with perpendicular, secondary ridges (apotypic).*

Pupal abdominal sutures are simple in most species (Fig. 4.42); however, those of *D. nipponica*[1] and *D. shasta* bear a series of perpendicular, secondary ridges, extended perpendicular to the suture (Fig. 4.40). This similarity is considered convergent.

Character 11. *abdominal tergites without transverse, raised, darkly sclerotized bands (plesiotypic) / abdominal tergites (at least segments I-II) with transverse, raised, darkly sclerotized bands on either side of midline (apotypic).*

Pupae of both *D. nipponica* (Fig. 4.26) and *D. bicarinata* (Fig. 4.22) possess transverse, raised, darkly sclerotized bands on the abdominal tergites; however, species differ in that bands are on segments I-VII in *D. nipponica*, but only segments I and II in *D. bicarinata*. Although a transformation series is suggested, other characters indicate the apotypic condition has arisen independently in these two species. Both phylogenies (Figs. 1, 2) accept the latter interpretation.

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[1] Based on examination of a single specimen.

6.4.3 Adult

Character 12. *male antenna short, its length less than 7mm, and with antennal f4 only ca. 90 times the length of the pedicel (plesiotypic) / male antenna elongate, its length 8mm or more, and with antennal f4 at least 110 times the length of the pedicel (apotypic).*

Except for character 14 (see below), this is considered the most informative character included in this analysis. The markedly elongate antennae of an adult male is one of the striking synapotypies of the Deuterophlebiidae. Although antennae of both *D. brachyrhina* Courtney and *D. oporina* Courtney are elongate, they are substantially shorter than those of all other species of mountain midge. Comparison of the relative length of antennal articles demonstrates that most difference is related to the length of antennal flagellomere 4 (*f4*). The plesiotypic state is considered an intermediate stage in the transformation from a more or less "normal" nematoceran antenna (*e.g.*, comparable to a blephariceríd anntenna) to that of more derived members of the Deuterophlebiidae. The apotypic state helps define the latter group of species.

Character 13. *postgena and oral region bearing microtrichia (plesiotypic) / postgena and oral region glabrous (apotypic).*

The plesiotypic condition is typical of most primitive species of mountain midge, and apparently of the Blephariceridae and other nematocerous flies. The presence of a glabrous postgena and oral region helps define a rather large derivative clade, including *D. nipponica*, and the *tyosenensis* and *coloradensis* species groups. However, the apotypic state also occurs in *D. brachyrhina*, presumably by convergence. Although the latter may suggest homoplastic tendencies, the character is considered a moderately important indicator of phylogenetic relationship.

Character 14. *male tibia and tarsus without capitate macrotrichia (plesiotypic) / male tibia and tarsus bearing capitate macrotrichia along ventral margin (apotypic).*

The ventral margin of the tibia and tarsus in most mountain midges bears numerous capitate macrotrichia (Figs. 4.58, 4.64). I have argued (Courtney *in press 2*) that the presence of capitate macrotrichia is an adaptation to the males' exclusively aerial life above torrential habitats. Male deuterophlebiids generally fly at or near the stream surface, usually over turbulent reaches, which often results in their being knocked into the water. Recovery is usually rapid, with males able to resume flight within a few seconds. I hypothesized that this ability is related to the mechanical and hydrofuge properties of elongate appendages, particularly those with capitate macrotrichia (*i.e.*, legs). Similar structures, including long, filiform antennae, and legs with enlarged empodia or without tarsal claws, are seen in males of some surface-skating flies. The bent-tipped, or L-shaped, hairs on water strider (Heteroptera: Gerridae) legs presumably serve a similar role.

Among deuterophlebiids, capitate macrotrichia are lacking only in *D. brachyrhina* (Fig. 4.63). This condition is typical of all other Diptera, as well as all other insects. The apotypic state is both unique and innovative, and considered a strong indicator of the monophyly of the Deuterophlebiidae, exclusive of *D. brachyrhina*. This character provides compelling evidence that *D. brachyrhina* is the sister group of all other mountain midges.

Character 15. *male gonostylus short, its length subequal to length of dorsal plate, and with ventromedial margin more or less straight (plesiotypic) / male gonostylus elongate, its length greater than length of dorsal plate, and with ventromedial margin sinuate (apotypic).*

Unlike in most Diptera, genitalia furnish little phylogenetic information in deuterophlebiids. Marked fusion of structures has obscured segmental boundaries and lead to a rather simple arrangement. However, certain features of the male genitalia provide insights on relationships among plesiotypic lineages. One pertains to the structure of the gonostylus. In *D. brachyrhina*, *D. oporina*, and *D. inyoensis*, gonostyli are short and relatively unmodified, with the ventromedial margin more or less even. In other species, gonostyli are elongate, distinctly tapered apically, and have a sinuate ventromedial margin. The latter, presumedly apotypic, state is given in support of the monophyly of the Deuterophlebiidae, exclusive of the above three species.

6.5 Zoogeographic Considerations

Among Nearctic mountain midges, both *D. inyoensis* and *D. coloradensis* are widespread in western North America, but noticeably absent from northern and central British Columbia (see Figs. 4.82, 4.84). This suggests a vicariant pattern, with Beringian and "southern" elements. Because disjunct populations show little evidence of morphological divergence, a late Wisconsinan vicariant event, presumably involving glaciation, is suggested. Alternatively, and more likely, this distributional gap reflects the inaccessibility of northern and central British Columbia, and concomitant lack of collecting.

One of the more puzzling discoveries is the paucity of deuterophlebiid records from Alaska. Streams in the Brooks, Alaska, and Chugach Ranges contain seemingly suitable habitats, yet neither deuterophlebiids nor blephariceridis are present (*personal observation*). The absence of blephariceridis is particularly enigmatic, since these flies are widespread and apparently much more vagile than are deuterophlebiids.

Among other Nearctic species, only *D. personata* is widespread (see Fig. 4.83). As in *D. inyoensis* and *D. coloradensis*, the distribution of *D. personata* suggests a vicariant pattern, with most records from California, Oregon, Washington and southern British Columbia, but also a single population in the southern Yukon. Populations from Washington, British Columbia, and the Yukon consist exclusively of females (Courtney *in press 2*), providing strong evidence of geographic parthenogenesis.

Deuterophlebiids are also widespread in mountainous areas of the central and eastern Palaearctic, with species known from the Himalaya, Tien Shan, Altai, and other ranges in Asia, and from Korea and Japan (see Fig. 4.81). At present, no Holarctic species are known; this could be a collecting artifact, since records for the northeastern Palaearctic are almost non-existent.

Amphi-Pacific distributions, as seen in mountain midges, are typical of several aquatic and/or montane insect groups. The black fly genus *Gymnopais*; caddisfly family Uenoidae, Trout-stream beetles (Amphizoidae) and ice-crickets (Grylloblattidae) are among the best known examples. Several genera of blephariceridds (*Agathon, Bibiocephala, Philorus*) exhibit comparable distributions. Unfortunately, the phylogenetic relationships both within and among these genera has not been determined, and the biogeographic significance of their distributions remains unclear.

The "accepted" phylogeny (Fig. 1) predicts that the Nearctic fauna is not monophyletic. Superposition of this phylogeny and contemporary species distributions results in an area cladogram (Fig. 3) that suggests the Nearctic fauna is the result of either three separate invasions of North America (*i.e.*, ancestral- *D. inyoensis, D. shasta + D. personata* (*i.e.*, part of *tyosenensis* group), and *coloradensis* group) or, alternatively, two invasions of North America (ancestral- *D. inyoensis* and *tyosenensis + coloradensis* groups), with subsequent re-invasion of the Palaearctic by part of the *tyosenensis* group. Any interchanges presumably occurred via the Beringian land bridge, during the Tertiary or early Pleistocene.

6.6 Conclusions

Hypotheses about the relationships of constituent species of the Deuterophlebiidae are presented as alternate cladograms (Figs. 1, 2). In both reconstructions, early dichotomies are based primarily on features of the adult male; namely, capitate leg macrotrichia, elongation of the male antenna, and gonostylus structure. Both phylogenies include the same unresolved tritomy, two branches of which represent species known only as adults (*D. blepharis* and *D. mirabilis*).

Alternate reconstructions differ mostly with respect to derivative clades. Phylogeny I (Fig. 1) emphasizes the presence of pupal mesothoracic spines, which defines the *tyosenensis* species group. Unfortunately, pupae are unknown (or unassociated with adults) in the Palaearctic species *D. brachyrhina*, *D. oporina*, *D. blepharis* and *D. mirabilis*. In phylogeny II (Fig. 2), derivative clades are resolved mostly by larval chaetotaxy. Excluding *D. inyoensis*, this results in a monophyletic Nearctic fauna, but at the expense of a second tritomy. Larvae are unknown (or unassociated with adults) in four Palaearctic species, and character states have not been determined for another two Palaearctic species (due either to incomplete descriptions or lack of material for examination). Hypotheses emphasizing larval characters are, therefore, rather tenuous, and phylogeny I is favoured. Both phylogenies were run through MacClade, with both giving consistency indices between ca. 0.70 - 0.75, depending on character weighting.

Because of large gaps in our knowledge about the Palaearctic deuterophlebiid fauna, phylogenetic and zoogeographic hypotheses are tentative. Discovery of the the immature stages of all Palaearctic mountain midges, especially the plesiotypic species *D. brachyrhina* and *D. oporina*, are exciting future prospects for testing the hypotheses generated in the present analysis.

Table 1. Matrix of characters analyzed to determine phylogenetic relationships of the Deuterophlebiidae.

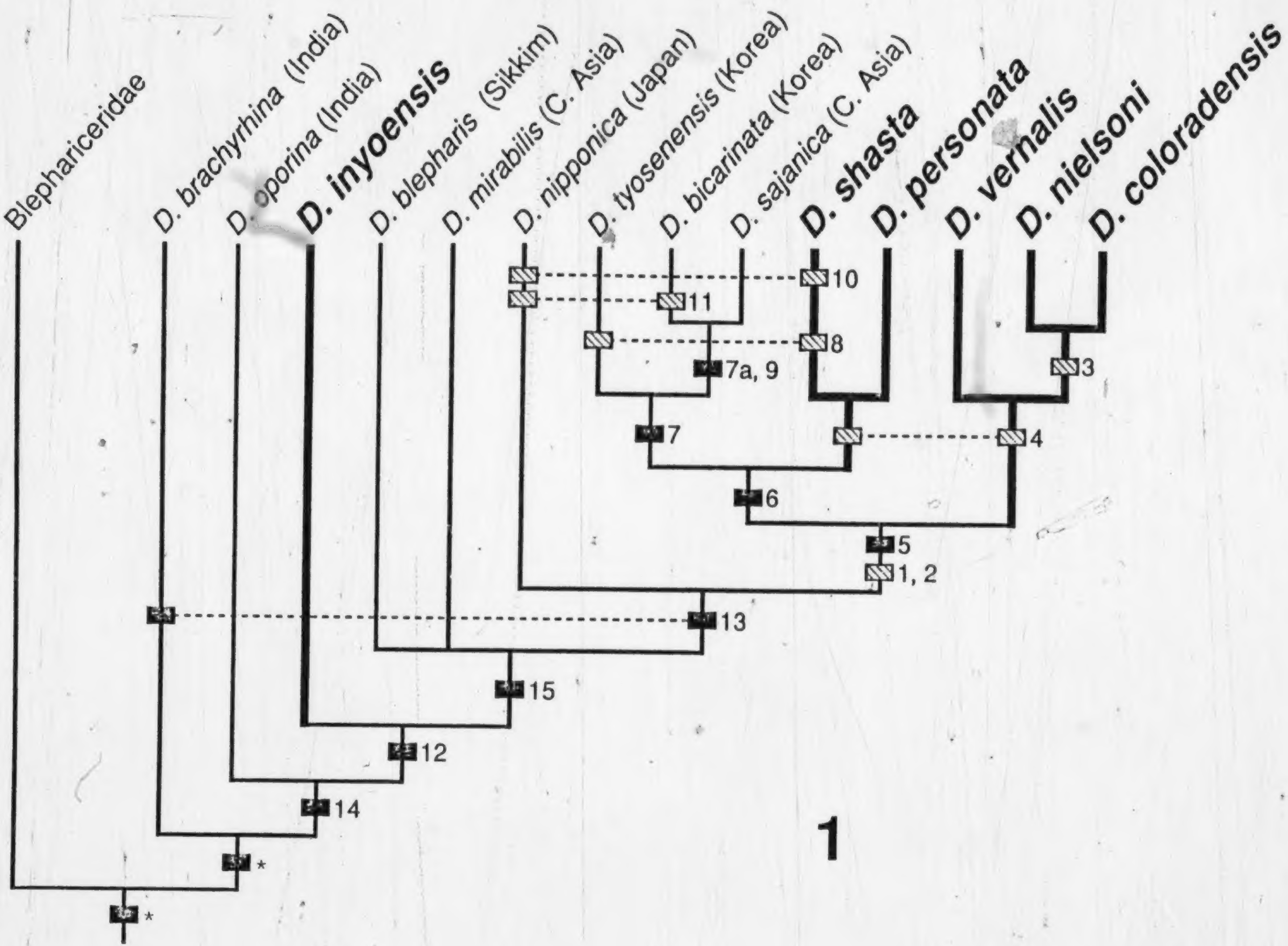
"0" = plesiotypic
"1" = apotypic
"2" = apotypic (i.e., subsequent stage in transformation sequence)

"?" = character state unknown
"-" = not applicable

Taxon/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Blephariceridae [Outgroup]	0	0	0	-	-	0	-	0	0	0	0	0	0	0	-
D. brachyrhina	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0
D. oporina	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0
D. inyoensis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
D. blepharis	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1
D. mirabilis	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1
D. nipponica	?	?	0	?	0	0	0	0	?	1	1	1	1	1	1
D. tyosenensis	?	?	0	?	?	1	1	1	?	0	0	1	1	1	1
D. bicarinata	1	1	0	0	?	1	2	0	1	0	1	1	1	1	1
D. sajanica	1	1	0	0	?	1	2	0	1	0	0	1	1	1	1
D. shasta	0	0	0	1	1	1	0	1	0	1	0	1	1	1	1
D. personata	1	1	0	1	1	1	0	0	0	0	0	1	1	1	1
D. vernalis	1	1	0	1	1	0	0	0	0	0	0	1	1	1	1
D. nielsoni	1	1	1	1	1	0	0	0	0	0	0	1	1	1	1
D. coloradensis	1	1	1	1	1	0/1	0	0	0	0	0	1	1	1	1

Figure 1. Phylogeny I - hypothesized phylogenetic relationships of the world species of Deuterophlebiidae, with derivative clades resolved mostly by pupal mesonotal spines. Primary apotypies indicated by solid squares, and secondary apotypies by hatched squares; dashed lines refer to proposed convergences. Nearctic species shown in bold type. Asterisks refer to characters fully discussed in chapters 2 and 3.

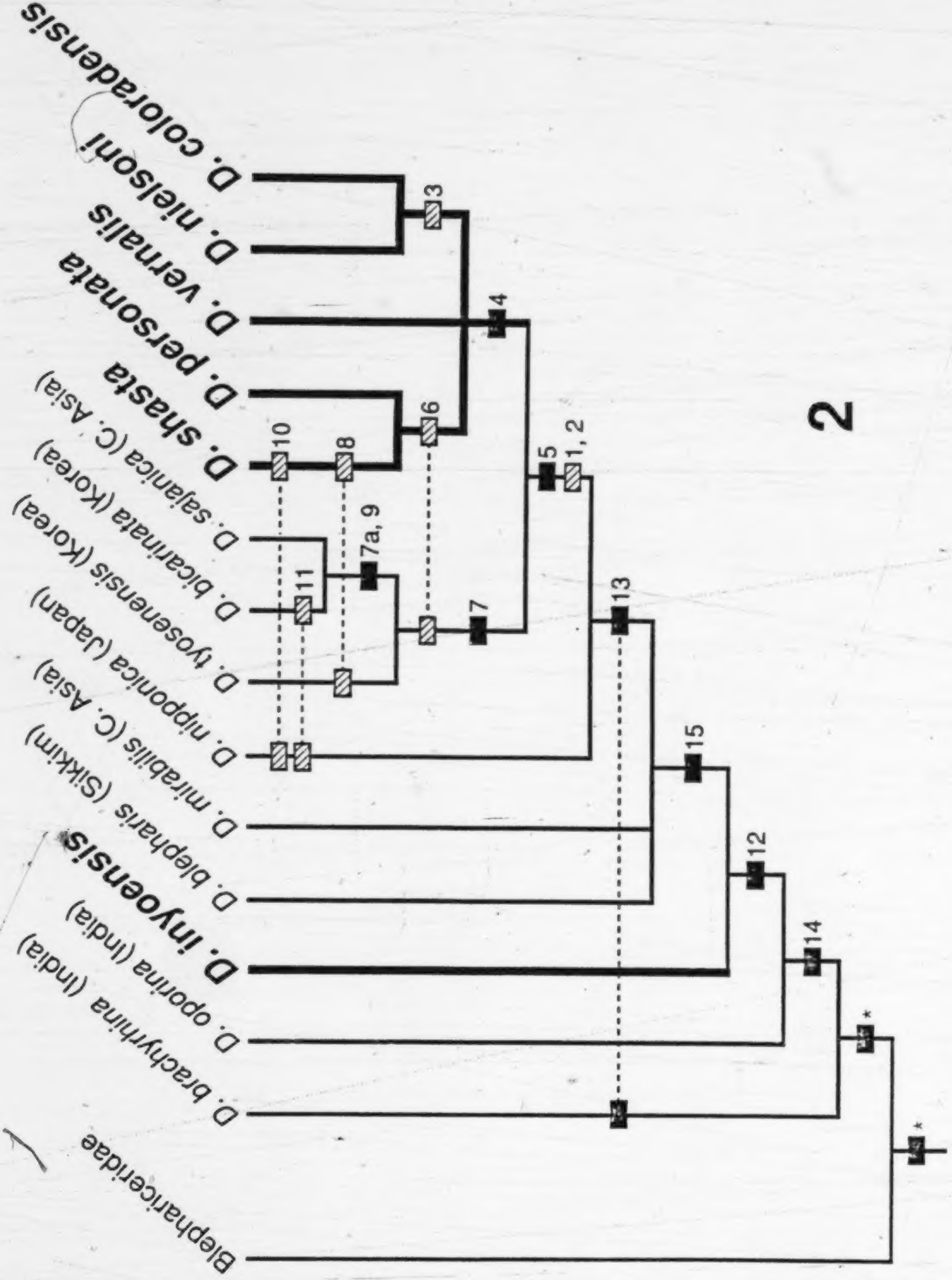
Apotypies: **1**, sensilla prl branched; **2**, sensilla at and mt branched; **3**, clypeal lobe uniformly pale; **4**, sensilla group ap with only two digitiform sensilla; **5**, instar II proleg with four rows of crochets; **6**, mesonotum with spines above gill; **7**, gill in the form of three lateral filaments and one posteriorly projected filament; **7a**, gill with posterior filament elongate, ca. twice as long as broad; **8**, abdominal tergites without microtubercles; **9**, abdominal tergites with microtrichia randomly distributed over cuticle; **10**, abdominal suture with perpendicular, secondary ridges; **11**, abdominal tergites with transverse, raised, darkly sclerotized bands on either side of midline; **12**, male antenna elongate, and antennal f4 at least 110 times the length of the pedicel; **13**, postgena and oral region glabrous; **14**, male tibia and tarsus with capitate macrotrichia; **15**, male gonostylus elongate, with ventromedial margin sinuate.


Blephariceridae
D. brachyrhina (India)
D. oporina (India)
D. inyoensis
D. blepharis (Sikkim)
D. mirabilis (C. Asia)
D. nipponica (Japan)
D. tyosenensis (Korea)
D. bicarinata (Korea)
D. sajanica (C. Asia)
D. shasta
D. personata
D. vernalis
D. nielsoni
D. coloradensis
10
11
8
7a, 9
3
7
4
6
5
1, 2
13
15
12
14
*
*

1

Figure 2. Phylogeny II - hypothesized phylogenetic relationships of the world species of Deuterophlebiidae, with derivative clades resolved mostly by larval chaetotaxy. Primary apotypies indicated by solid squares, and secondary apotypies by hatched squares; dashed lines refer to proposed convergences. Nearctic species shown in bold type. Asterisks refer to characters fully discussed in chapters 2 and 3.

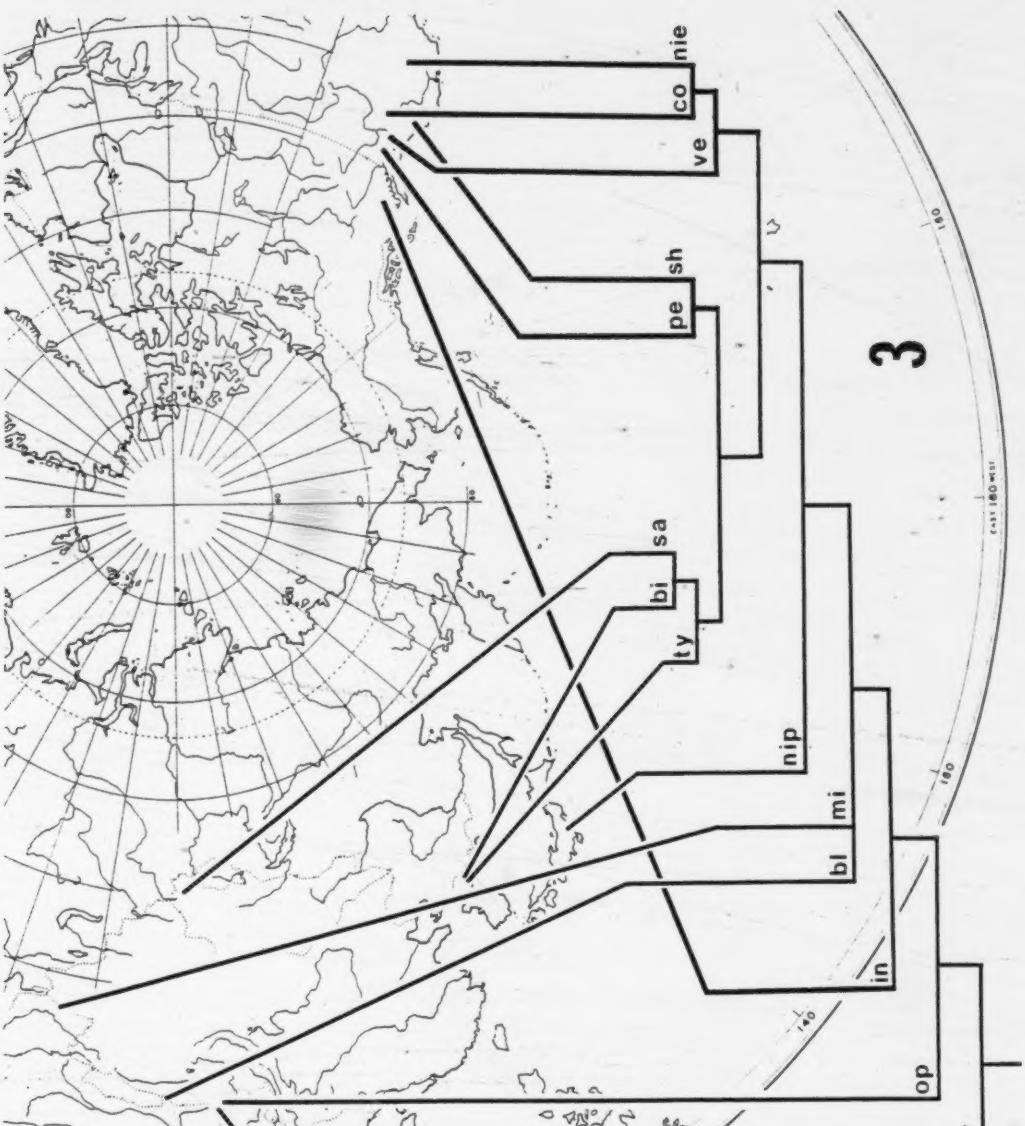
Apotypies: 1, sensilla prl branched; **2**, sensilla at and mt branched; **3**, clypeal lobe uniformly pale; **4**, sensilla group ap with only two digitiform sensilla; **5**, instar II proleg with four rows of crochets; **6**, mesonotum with spines above gill; **7**, gill in the form of three lateral filaments and one posteriorly projected filament; **7a**, gill with posterior filament elongate, ca. twice as long as broad; **8**, abdominal tergites without microtubercles; **9**, abdominal tergites with microtrichia randomly distributed over cuticle; **10**, abdominal suture with perpendicular, secondary ridges; **11**, abdominal tergites with transverse, raised, darkly sclerotized bands on either side of midline; **12**, male antenna elongate, and antennal f4 at least 110 times the length of the pedicel; **13**, postgena and oral region glabrous; **14**, male tibia and tarsus with capitate macrotrichia; **15**, male gonostylus elongate, with ventromedial margin sinuate.


Blephariceridae
D. brachyrhina (India)
D. oporina (India)
D. inyoensis
D. blepharis (Sikkim)
D. mirabilis (C. Asia)
D. nipponica (Japan)
D. tyosenensis (Korea)
D. bicarinata (Korea)
D. sajanica (C. Asia)
D. shasta
D. personata
D. vernalis
D. nielsoni
D. coloradensis
10
11
8
7a, 9
6
3
4
7
5
1, 2
13
15
12
14
*
*

2

Figure 3. Area cladogram of the world species of Deuterophlebiidae, based on hypothesized phylogenetic relationships from Figure 1.

Species abbreviations: **bi,** *D. bicarinata*; **bl,** *D. blepharis*; **br,** *D. brachyrhina*; **co,** *D. coloradensis*; **in,** *D. inyoensis*; **mi,** *D. mirabilis*; **nie,** *D. nielsoni*; **nip,** *D. nipponica*; **op,** *D. oporina*; **pe,** *D. personata*; **sa,** *D. sajanica*; **sh,** *D. shasta*; **ty,** *D. tyosenensis*; **ve,** *D. vernalis*.


nie
co
ve
sh
pe
sa
bi
ty
nip
mi
bl
in
op
br
3
160
EAST 180 WEST
160
140

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7. GENERAL CONCLUSIONS

The title of this dissertation, "Morphology, systematics and ecology of mountain midges (Diptera: Deuterophlebiidae)", may sound somewhat pretentious, or perhaps too general. However, research in systematic biology should, and typically does, incorporate knowledge from a variety of disciplines, not the least of which are comparative morphology and ecology. A thorough understanding of the structure of all semaphoronts, and the mechanisms by which the environment influences their structures, is essential for elucidating the phylogeny and evolutionary direction of a taxon. Admittedly, mastery of this broad array of topics can be an arduous and, sometimes, impossible task. None-the-less, this investigation of mountain midges has aspired to succeed in this holistic approach.

At the outset, the objectives, and manner in which to proceed toward these objectives, seemed straight-forward, particularly since the taxon of interest was relatively small. But, as happens in many scientific endeavors, realization of objectives met innumerable difficulties resulting in tangential investigations. Although intending to resolve a few simple questions, it is apparent that this study has only scratched the surface of a morass of additional, unresolved questions. However, this project has successfully answered many of those original questions, and provided a foundation upon which future investigations may build.

Mountain midges are rheophilic specialists, possessing a variety of morphological and ecological features that permit life in swiftly flowing, often torrential, streams. The goal of the initial phase of this project was to provide morphological information about one of the most specialized and least known life stages, the larva. This study provided a basis for detailed descriptions of, and proposed homologies for, musculature and external features of the head capsule. It also provided a foundation for discussions of feeding behaviour in deuterophlebiids, and other larval Diptera (especially Blephariceridae). In addition, external structure of the thorax and abdomen was described, and a system for chaetotaxy of deuterophlebiid larvae presented.

Morphological data was the primary basis for cladistic analysis of larval, pupal and adult features of the Deuterophlebiidae and related Diptera, and provided support for: (1) monophyly of the Blephariceroidea (= Deuterophlebiidae + Blephariceridae); (2) monophyly of the Blephariceromorpha (= Nymphomyiidae + (Deuterophlebiidae + Blephariceridae); and (3) a sister-group relationship between the Blephariceromorpha and Psychodomorpha.

On placing mountain midges within the framework of higher classification of Diptera, the logical "next step" was to examine, in greater detail, the classification of the ingroup (*i.e.*, Deuterophlebiidae). Taxonomic revision of the world species of mountain midges led to discovery of six new species. Four are Palaearctic: *D. bicarinata* sp. nov. from southern Korea, and *D. brachyrhina* sp. nov., *D. oporina* sp. nov., and *D. blepharis* sp. nov. from the Himalaya of Sikkim and northeastern India (Assam). Two are Nearctic: *D. personata* sp. nov., which is widespread in western North America, with northern populations apparently parthenogenetic; and *D. vernalis* sp. nov. from south-central Washington state. The revision included descriptions of all species of mountain midges, and designation of a lectotype for *D. mirabilis* Edwards, and a lectotype and paralectotype for *D. coloradensis* Pennak. Distributional data and keys to larvae, pupae, and adults for all species, and a general discussion of character variation, were provided.

In many respects, taxonomy and ecology are inseparable. Species definitions rely on knowledge of reproductive isolation and chorology (sympatry *vs.* allopatry), and this type of information provides valuable insights into the evolutionary direction of a taxon. In this study of mountain midges, ecological investigations emphasized the habitat requirements, reproductive biology, and phenologies of Nearctic deuterophlebiids. Mountain midges were shown to inhabit a wider variety of streams than was previously thought. Although adults demonstrate marked diel synchrony, with emergence, flight, and mating during the early morning, deuterophlebiid populations typically have asynchronous life histories (*i.e.*, at least in Nearctic species). This is particularly adaptive in mountain streams, where frequent, unpredictable flooding may cause substrate scouring, and high mortality of larvae and pupae. Temporal isolation of torrenticolous insect populations was demonstrated, especially among sympatric deuterophlebiids and blephariccrids; however, the exact mechanism responsible for this isolation remains unclear.

Another aspect of the ingroup analysis focused on the phylogenetic relationships of constituent species. Cladistic analysis of larval, pupal, and adult characters provided a framework for discussion about the phylogeny and zoogeography of world species of Deuterophlebiidae. Preliminary zoogeographic analyses suggests that Nearctic deuterophlebiids originated from at least two invasions of North America. Readers may feel that some of my phylogenetic and zoogeographic hypotheses are ill-founded or premature, especially since data for most Palaearctic species are sorely lacking. Even if my hypotheses are premature, I believe they are testable and provide a framework upon which future investigations can build. If this study is impetus for future research on the Deuterophlebiidae, my primary objective will have been realized.

"I am not concerned that my hypotheses may be proven invalid. I am concerned that they might not even be tested."[1]

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[1] From: Ball, G..E. 1978. The species of the Neotropical genus *Trichopselaphus* Chaudoir (Coleoptera: Carabidae: Harpalini): classification, phylogeny and zoogeography. *Quaestiones Entomologicae* 14: 447-489. [quote from pg. 470]

APPENDIX A

Selected characters of non-deuterophlebiid Diptera.

Figures 1-6. Selected characters of Blephariceridae larvae.

Figure 1. *Agathon comstocki* instar I larva, apex of antenna; scale bar = 4μm.

Figure 2. *Bibiocephala grandis* instar I larval mouthparts, showing apex of "unworn" mandibular lobes (ventral view); scale bar = 10μm.

Figure 3. *Bibiocephala grandis* instar I larval mouthparts, showing unworn mandible (frontolateral view); scale bar = 10μm.

Figure 4. *Bibiocephala grandis* instar I larva, adoral margin of "worn" mandible (labrum removed); scale bar = 10μm.

Figure 5. *Blepharicera jordani* instar I larva, apex of lateral abdominal proleg; scale bar = 5μm.

Figure 6. *Agathon comstocki* instar I larva, apex of lateral abdominal proleg; scale bar = 5μm.

Abbreviations: *lr*, labrum; *md*, mandible; *mx*, maxilla; *prs*, prostheca.

1

md
mx
2

mx
3

md
4

5

6

Figures 7-12. Selected characters of Nematocera larvae.

Figure 7. Blephariceridae (*Agathon comstocki*) instar IV larva, adoral margin of newly molted mandible, showing lack of teeth wear; scale bar = 100µm.

Figure 8. Blephariceridae (*Agathon comstocki*) instar IV larva, adoral margin of older mandible, showing teeth wear; scale bar = 100µm.

Figure 9. Tipulidae (*Tipula* sp.) instar IV larva, adoral margin of mandible; scale bar = 100µm.

Figure 10. Tipulidae (*Antocha* sp.) instar IV larva, adoral margin of mandible; scale bar = 100µm.

Figure 11. Ptychopteridae (*Ptychoptera* sp.) instar IV larva, apical view of mandible; scale bar = 10µm.

Figure 12. Tipulidae (*Antocha* sp.) instar IV larval prementum and hypopharynx (ventral view); scale bar = 40µm.

Abbreviations: *hy*, hypopharynx; *lmpr*, prementum; *mdh*, basal mandibular hook/lobe; *mx*, maxilla; *prs*, prostheca.

7

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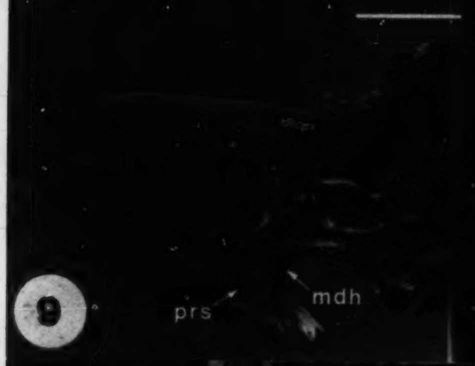
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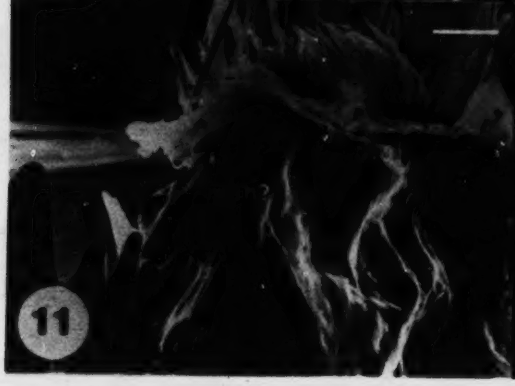
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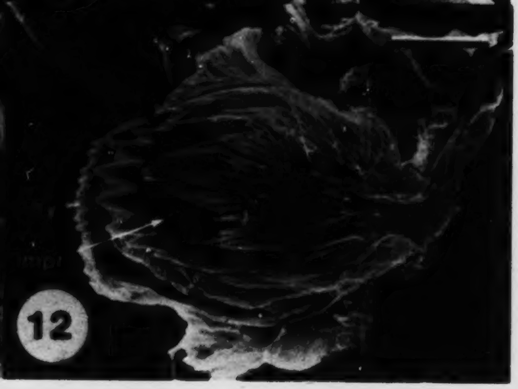

12

Figures 13-18. Selected characters of Nymphomyiidae (*Palaeodipteron walkeri*) larvae and pupae.

Figure 13. Nymphomyiidae instar IV larval mouthparts (ventral view); scale bar = 20μm.

Figure 14. Nymphomyiidae instar IV larval labrum-epipharynx (ventral view); scale bar = 10μm.

Figure 15. Nymphomyiidae instar IV larval mouthparts, showing anterior margin of postmentum, prementum (?), base of maxillae (ventral view); scale bar = 4μm.

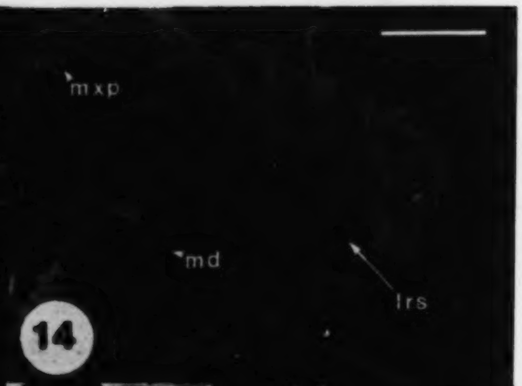
Figure 16. Nymphomyiidae instar IV larva, anal papillae (ventral view); scale bar = 20μm.

Figure 17. Nymphomyiidae instar IV larva, apex of lateral abdominal proleg, showing dimorphic crochets; scale bar = 10μm.

Figure 18. Nymphomyiidae pupa, showing prognathous head (lateral view); scale bar = 50μm.

Abbreviations: *lmpo*, postmentum; *lmpr*, prementum; *lms*, premental sclerite; *lr*, labrum; *lrs*, spatulate/pectinate labral macrotrichia; *md*, mandible; *mx*, maxilla; *mxp*, maxillary palp.

13



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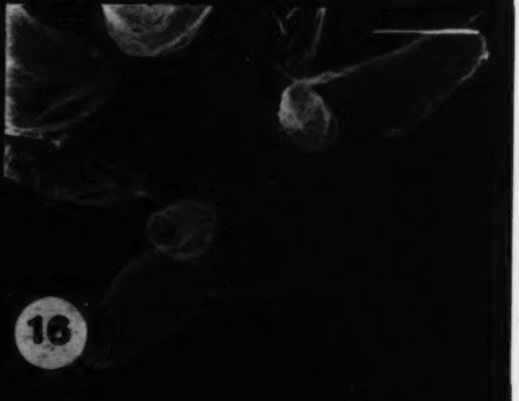

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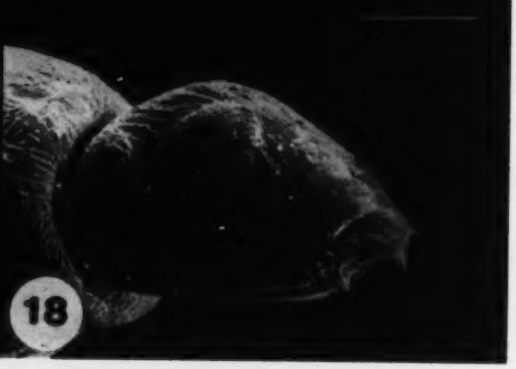

18

Figures 19-24. Selected characters of Nymphomyiidae (*P. walkeri*) adults.

Figure 19. Nymphomyiidae adult head (lateral view); scale bar = 40µm.

Figure 20. Nymphomyiidae adult head (frontal to slightly ventral view); scale bar = 40µm.

Figure 21. Nymphomyiidae adult, compound eye and lateral ocelli (lateral view); scale bar = 20µm.

Figure 22. Nymphomyiidae adult, medial margin of antenna; scale bar = 20µm.

Figure 23. Nymphomyiidae adult, acropod; scale bar = 4µm.

Figure 24. Nymphomyiidae adult, male genitalia (ventral view); scale bar = 20µm.

Abbreviations: *aed*, aedeagus; *aes*, aedeagal sheath; *emp*, empodium; *cib*, cibarium; *ley*, "lateral" ocelli (larval stemmata).

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APPENDIX B

Supplemental phenological data for Nearctic populations of Deuterophlebiidae.

Figure 1. Phenological data for Nestucca River population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 1a); numbers enclosed by brackets refer to sample sizes for each date.

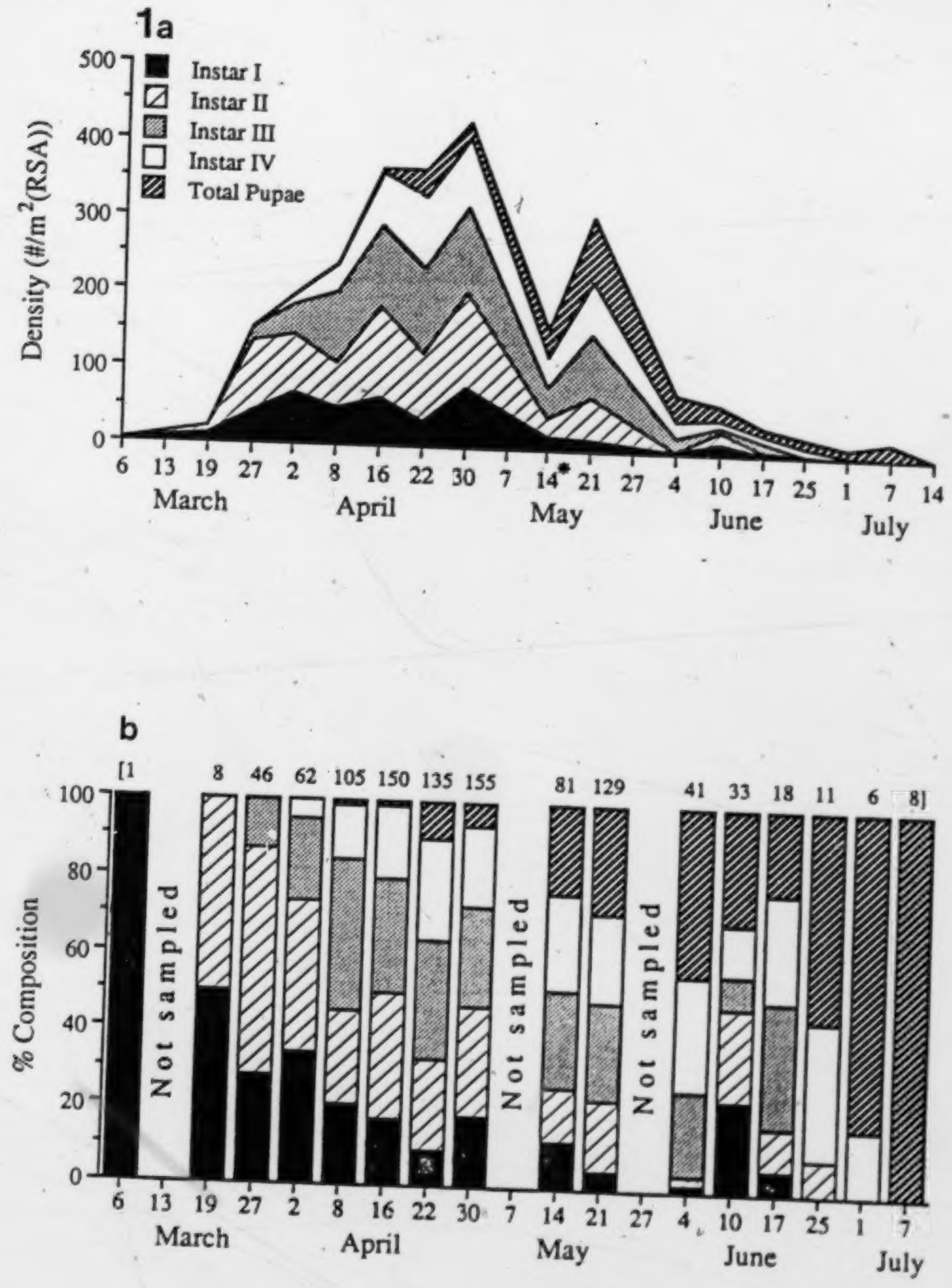

1a
500
400
300
200
100
0
Density (#/m^2(RSA))
Instar I
Instar II
Instar III
Instar IV
Total Pupae
6
13
19
27
2
8
16
22
30
7
14*
21
27
4
10
17
25
1
7
14
March
April
May
June
July
b
[1
8
46
62
105
150
135
155
81
129
41
33
18
11
6
8]
100
80
60
40
20
0
% Composition
Not sampled
Not sampled
Not sampled
6
13
19
27
2
8
16
22
30
7
14
21
27
4
10
17
25
1
7
March
April
May
June
July

Figure 2. Phenological data for Willamina Creek population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 2a); numbers enclosed by brackets refer to sample sizes for each date.

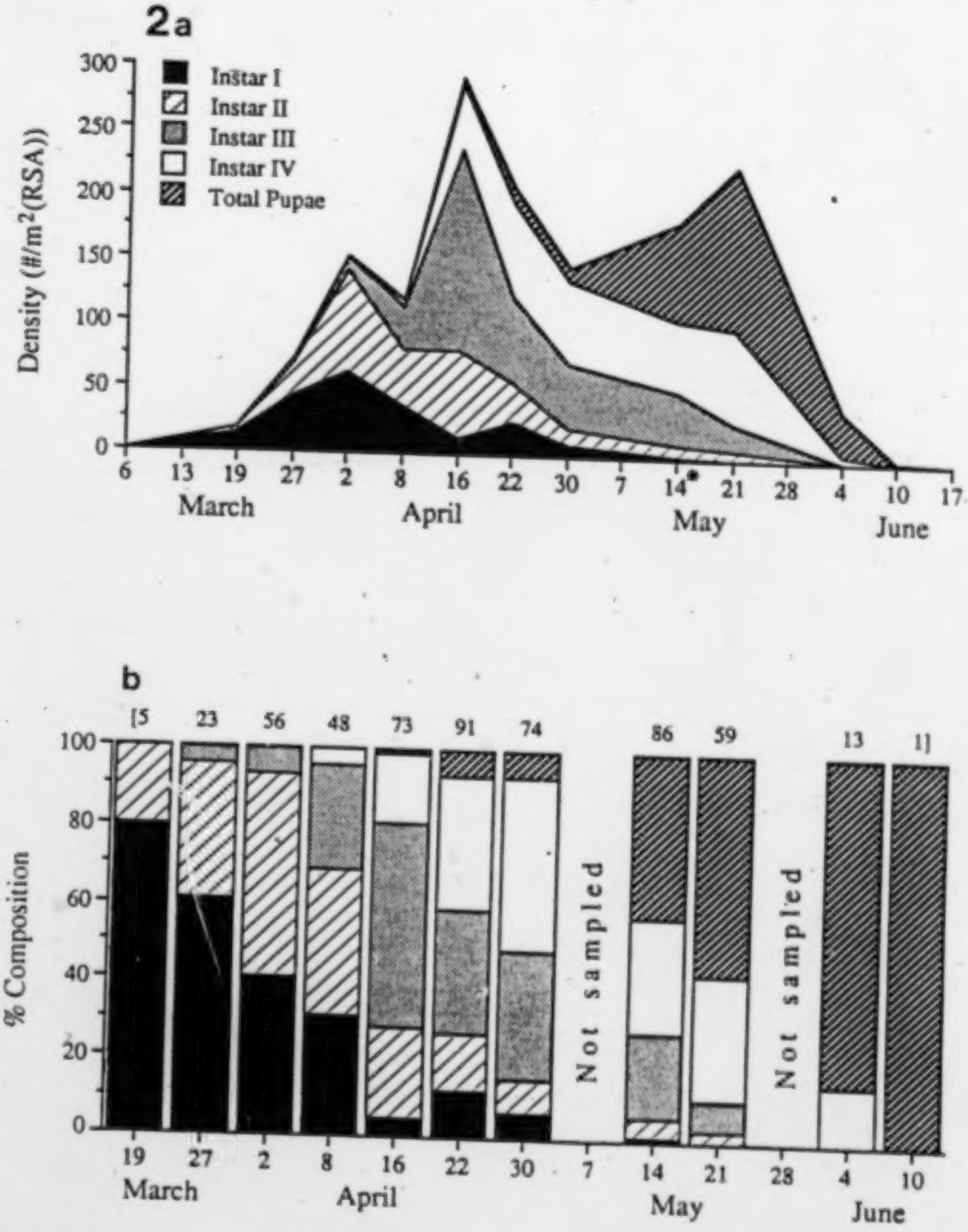
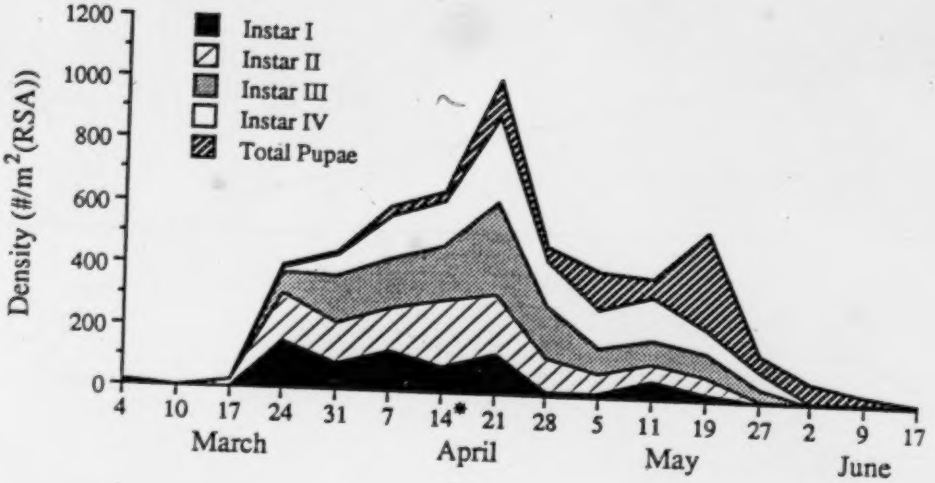

2a
Density (#/m²(RSA))
300
250
200
150
100
50
0
Instar I
Instar II
Instar III
Instar IV
Total Pupae
6
13
19
27
2
8
16
22
30
7
14
21
28
4
10
17
March
April
May
June
b
% Composition
100
80
60
40
20
0
[5
23
56
48
73
91
74
86
59
13
1]
Not sampled
Not sampled
19
27
2
8
16
22
30
7
14
21
28
4
10
March
April
May
June

Figure 3. Phenological data for Marys River population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 3a); numbers enclosed by brackets refer to sample sizes for each date.

3a


Instar I
Instar II
Instar III
Instar IV
Total Pupae
Density (#/m²(RSA))
1200
1000
800
600
400
200
0
4
10
17
24
31
7
14*
21
28
5
11
19
27
2
9
17
March
April
May
June

b

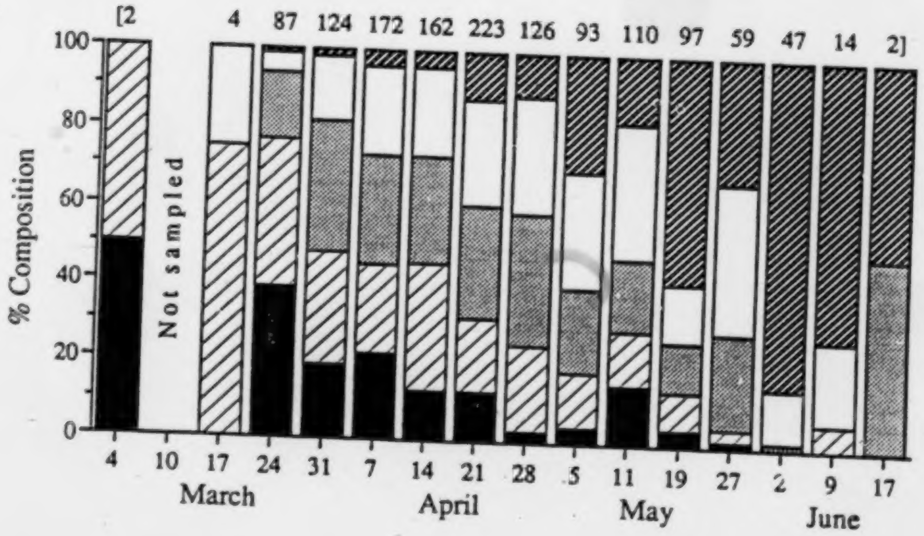

[2
4
87
124
172
162
223
126
93
110
97
59
47
14
2]
100
80
60
40
20
0
% Composition
Not sampled
4
10
17
24
31
7
14
21
28
5
11
19
27
2
9
17
March
April
May
June

Figure 4. Phenological data for Rock Creek population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 4a); numbers enclosed by brackets refer to sample sizes for each date.

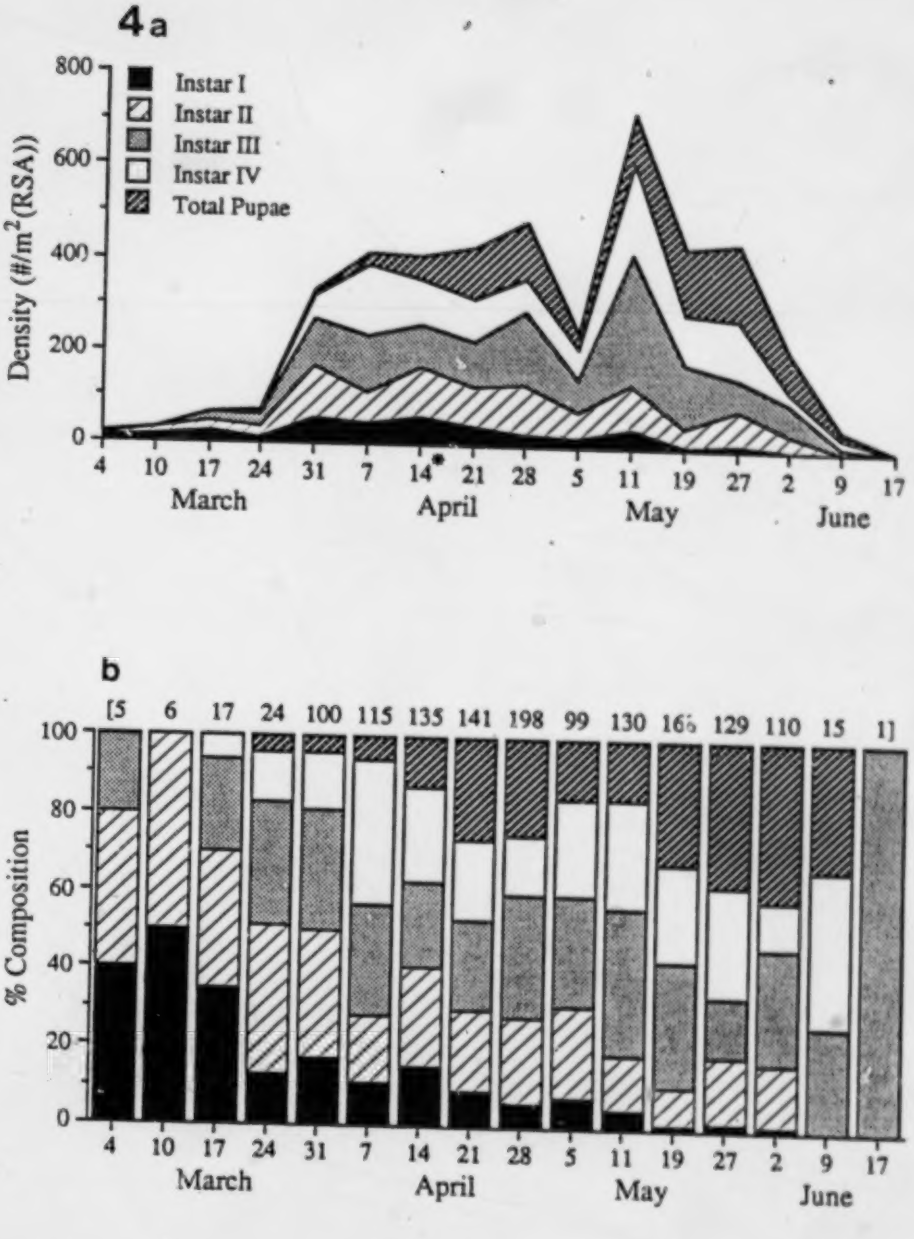

4a
800
600
400
200
0
Density (#/m^2(RSA))
Instar I
Instar II
Instar III
Instar IV
Total Pupae
4
10
17
24
31
7
14*
21
28
5
11
19
27
2
9
17
March
April
May
June
b
[5
6
17
24
100
115
135
141
198
99
130
166
129
110
15
1]
100
80
60
40
20
0
% Composition
4
10
17
24
31
7
14
21
28
5
11
19
27
2
9
17
March
April
May
June

Figure 5. Phenological data for Crooked Creek population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 5a); numbers enclosed by brackets refer to sample sizes for each date.

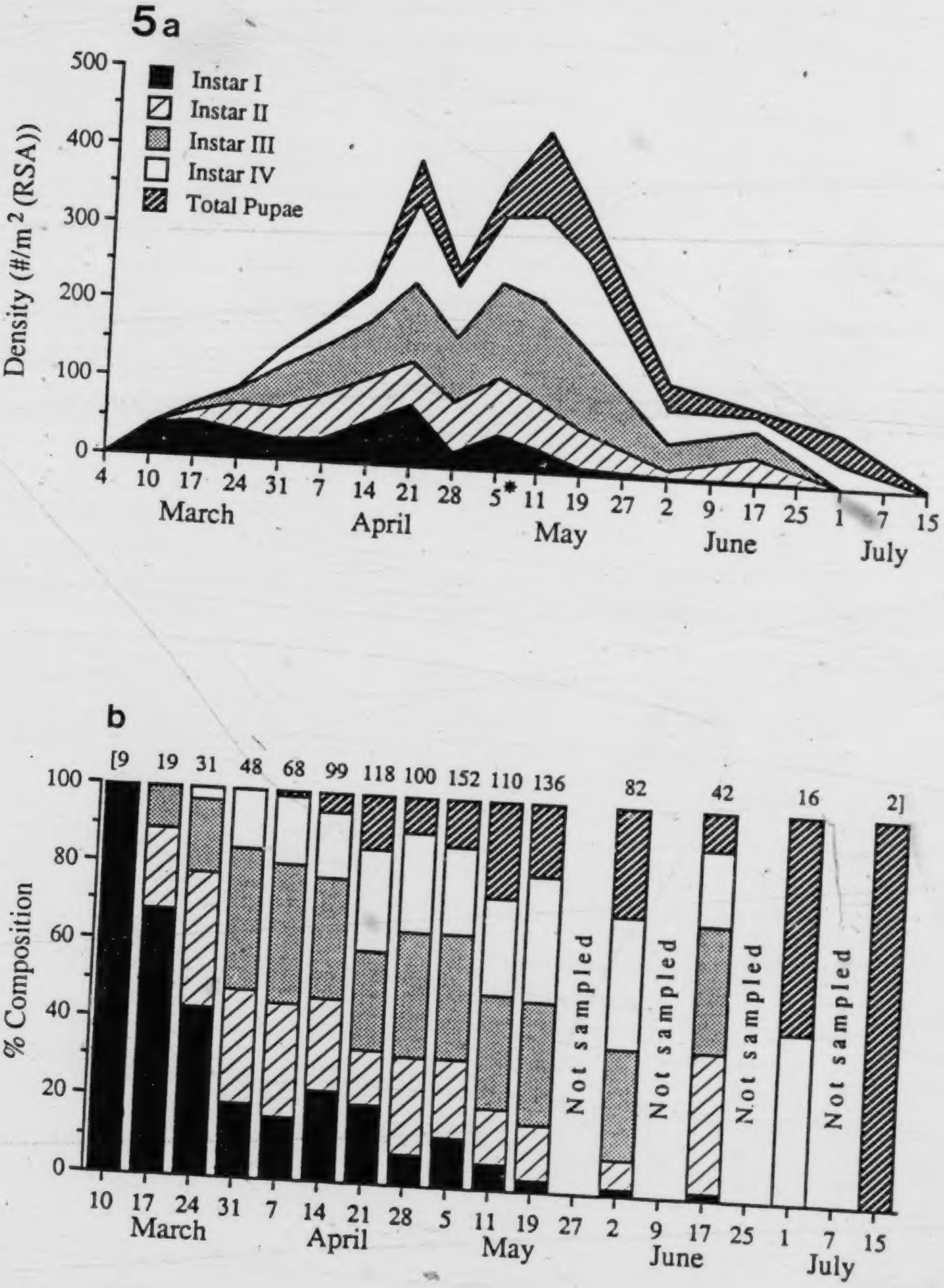
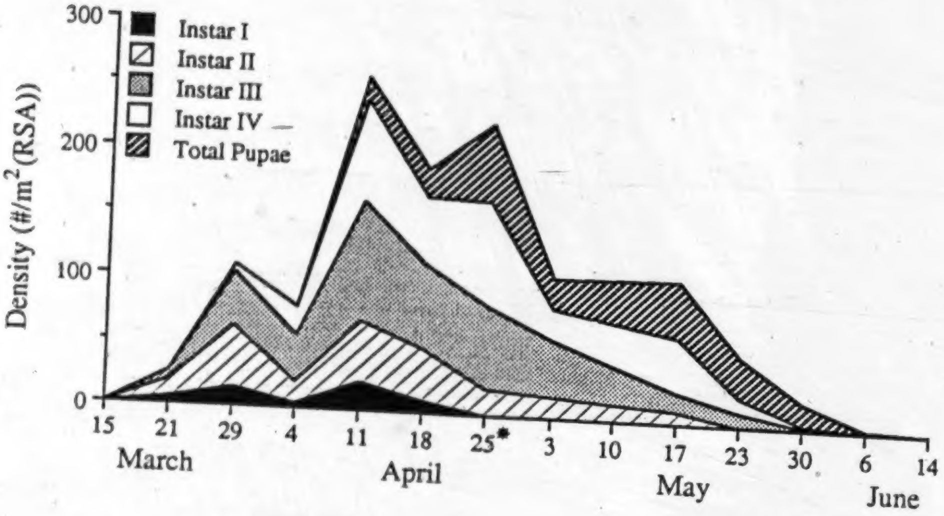

5a
Instar I
Instar II
Instar III
Instar IV
Total Pupae
Density (#/m^2 (RSA))
500
400
300
200
100
0
4 10 17 24 31 7 14 21 28 5* 11 19 27 2 9 17 25 1 7 15
March
April
May
June
July
b
[9 19 31 48 68 99 118 100 152 110 136 82 42 16 2]
% Composition
100
80
60
40
20
0
Not sampled
Not sampled
Not sampled
Not sampled
10 17 24 31 7 14 21 28 5 11 19 27 2 9 17 25 1 7 15
March
April
May
June
July

Figure 6. Phenological data for Wolf Creek population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 6a); numbers enclosed by brackets refer to sample sizes for each date.

6a


300
200
100
0
Density (#/m^2(RSA))
Instar I
Instar II
Instar III
Instar IV
Total Pupae
15
21
29
4
11
18
25*
3
10
17
23
30
6
14
March
April
May
June

b

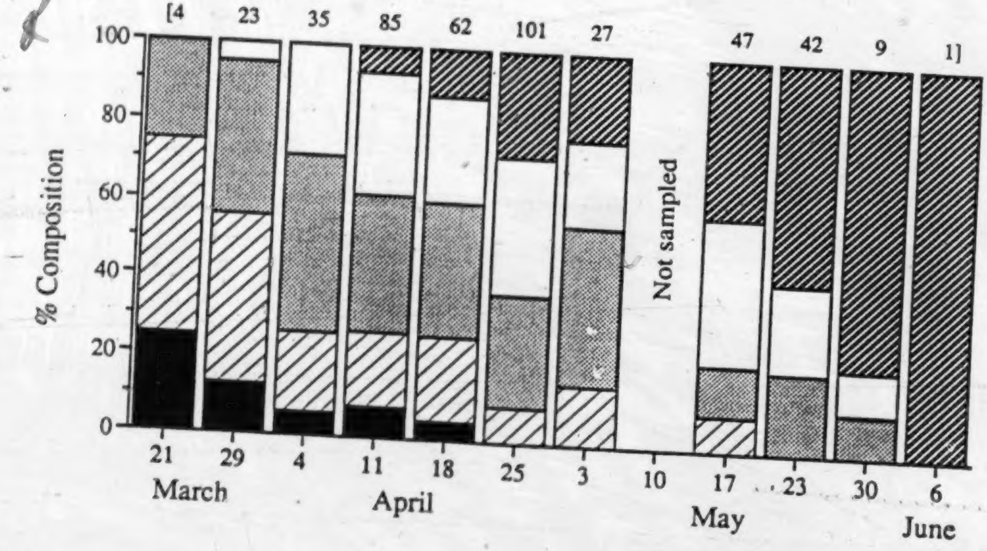
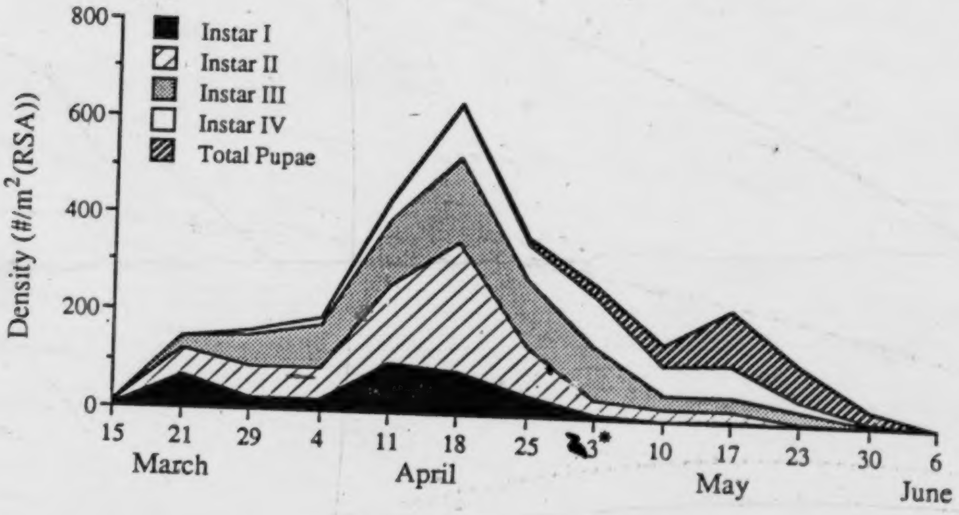

[4
23
35
85
62
101
27
47
42
9
1]
100
80
60
40
20
0
% Composition
Not sampled
21
29
4
11
18
25
3
10
17
23
30
6
March
April
May
June

Figure 7. Phenological data for Wildcat Creek population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 7a); numbers enclosed by brackets refer to sample sizes for each date.

7a


Instar I
Instar II
Instar III
Instar IV
Total Pupae
Density (#/m^2(RSA))
800
600
400
200
0
15
21
29
4
11
18
25
3*
10
17
23
30
6
March
April
May
June

b

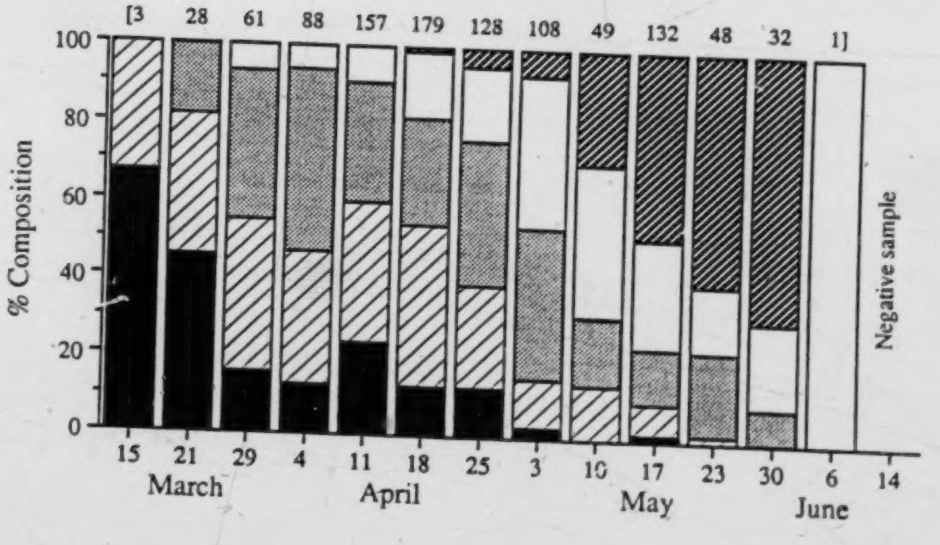
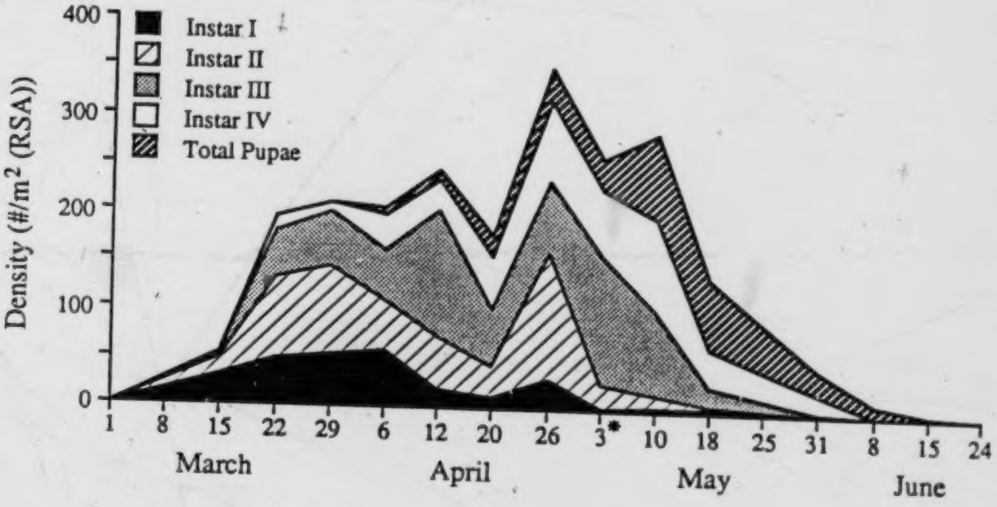

[3
28
61
88
157
179
128
108
49
132
48
32
1]
% Composition
100
80
60
40
20
0
15
21
29
4
11
18
25
3
10
17
23
30
6
14
March
April
May
June
Negative sample

Figure 8. Phenological data for Elk Creek population of *D. coloradensis*: (**a**) Area graph of pupal and larval instar density (number per square meter (rock surface area)) during 1986; asterisk refers to the initial appearance of adults; (**b**) Stacked bar graph of percent composition of pupal and larval instars during 1986 (patterns correspond to same instars as in Fig. 8a); numbers enclosed by brackets refer to sample sizes for each date.

8a


Instar I
Instar II
Instar III
Instar IV
Total Pupae
Density (#/m^2 (RSA))
400
300
200
100
0
1
8
15
22
29
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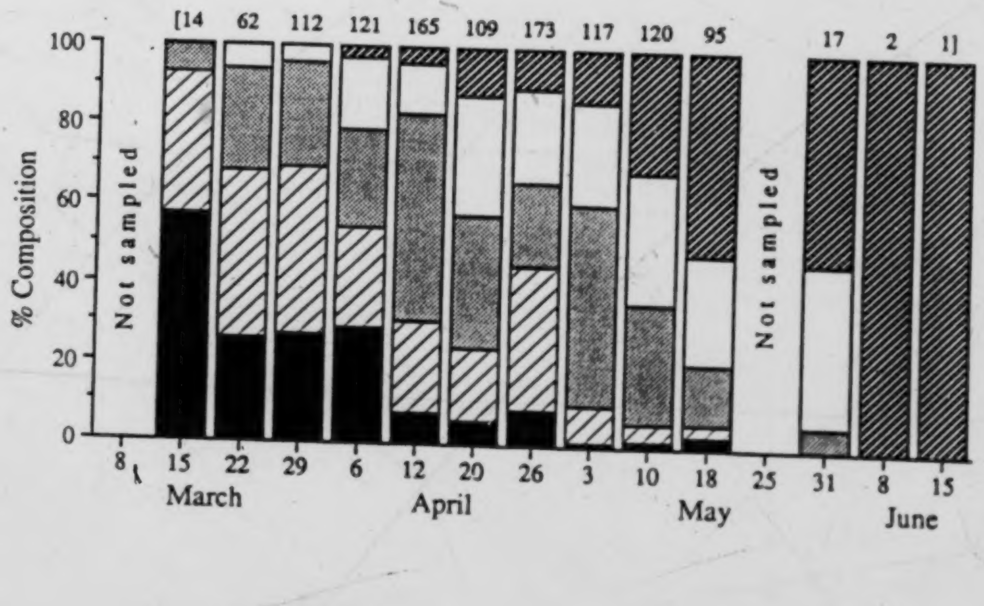
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